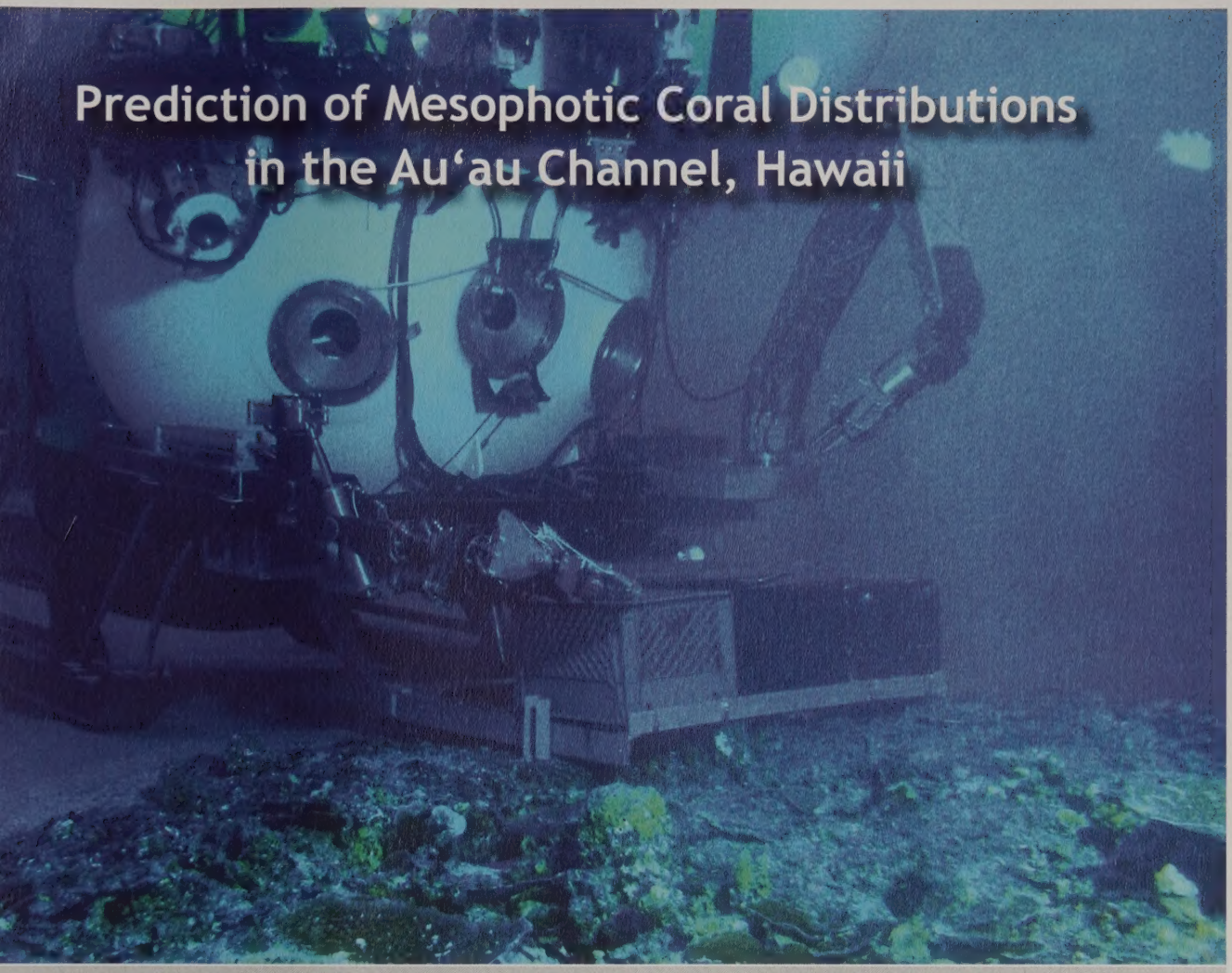
Prediction of Mesophotic Coral Distributions in the Au'au Channel, Hawaii



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Cover Photo: The Pisces V submersible working on a mesophotic reef of *Leptoseris hawaiiensis* corals on a small rock outcrop at a depth of 102 m. Photo Credit: HURL.

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ABOUT THIS DOCUMENT

This report describes the development and assessment of four spatially explicit predictive models describing mesophotic coral presence in the Au'au Channel Region in the Main Hawaiian Islands (MHI). This effort was conducted by NOAA's National Centers for Coastal Ocean Science (NCCOS) Biogeography Branch in partnership with NOAA's Hawaiian Islands Humpback Whale National Marine Sanctuary (HIHWNMS) and the NOAA Pacific Islands Fisheries Science Center (PIFSC). The surfaces resulting from this effort represent the first spatial predictions of mesophotic coral presence inside the Sanctuary. This report consists of five primary components: 1) an introduction to the HIHWNMS and its interest in mesophotic corals; 2) a description of the methods used to generate and validate the predictive mesophotic coral models; 3) a synopsis of the performance, accuracy and environmental relationships highlighted by these models; 4) a discussion of these environmental relationships and patterns, as well as a description of how these models can be applied for management decisions; and 5) a few concluding remarks about the study and about future research needs. These predictive surfaces will be used by the HIHWNMS and other local partners for planning research and monitoring activities, and will support the ecosystem based management and conservation of the HIHWHNMS.

For more information on this effort please visit: http://ccma.nos.noaa.gov/ecosystems/sanctuaries/hwnms/

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EXECUTIVE SUMMARY

The primary objective of this study was to predict the distribution of mesophotic hard corals in the Au'au Channel in the Main Hawaiian Islands (MHI). Mesophotic hard corals are light-dependent corals adapted to the low light conditions at approximately 30 to 150 m in depth. Several physical factors potentially influence their spatial distribution, including aragonite saturation, alkalinity, pH, currents, water temperature, hard substrate availability and the availability of light at depth. Mesophotic corals and mesophotic coral ecosystems (MCEs) have increasingly been the subject of scientific study because they are being threatened by a growing number of anthropogenic stressors. They are the focus of this spatial modeling effort because the Hawaiian Islands Humpback Whale National Marine Sanctuary (HIHWNMS) is exploring the expansion of its scope—beyond the protection of the North Pacific Humpback Whale (*Megaptera novaeangliae*)—to include the conservation and management of these ecosystem components. The present study helps to address this need by examining the distribution of mesophotic corals in the Au'au Channel region. This area is located between the islands of Maui, Lanai, Molokai and Kahoolawe, and includes parts of the Kealaikahiki, Alalākeiki and Kalohi Channels. It is unique, not only in terms of its geology, but also in terms of its physical oceanography and local weather patterns. Several physical conditions make it an ideal place for mesophotic hard corals, including consistently good water quality and clarity because it is flushed by tidal currents semi-diurnally; it has low amounts of rainfall and sediment run-off from the nearby land; and it is largely protected from seasonally strong wind and wave energy. Combined, these oceanographic and weather conditions create patches of comparatively warm, calm, clear waters that remain relatively stable through time.

Freely available Maximum Entropy modeling software (MaxEnt 3.3.3e) was used to create four separate maps of predicted habitat suitability for: (1) all mesophotic hard corals combined, (2) *Leptoseris*, (3) *Montipora* and (4) *Porites* genera. MaxEnt works by analyzing the distribution of environmental variables where species are present, so it can find other areas that meet all of the same environmental constraints. Several steps (Figure 0.1) were required to produce and validate four ensemble predictive models (i.e., models with 10 replicates each). Approximately 2,000 georeferenced records containing information about mesophotic coral occurrence and 34 environmental predictors describing the seafloor's depth, vertical structure, available light, surface temperature, currents and distance from shoreline at three spatial scales were used to train MaxEnt. Fifty percent of the 1,989 records were randomly chosen and set aside to assess each model replicate's performance using Receiver Operating Characteristic (ROC), Area Under the Curve (AUC) values. An additional 1,646 records were also randomly chosen and set

Image 1. A brightly colored school of reef fish inhabits a reef of *Leptoseris* corals at a depth of approximately 75 m in the Au'au Channel. Photo Credit: HURL.

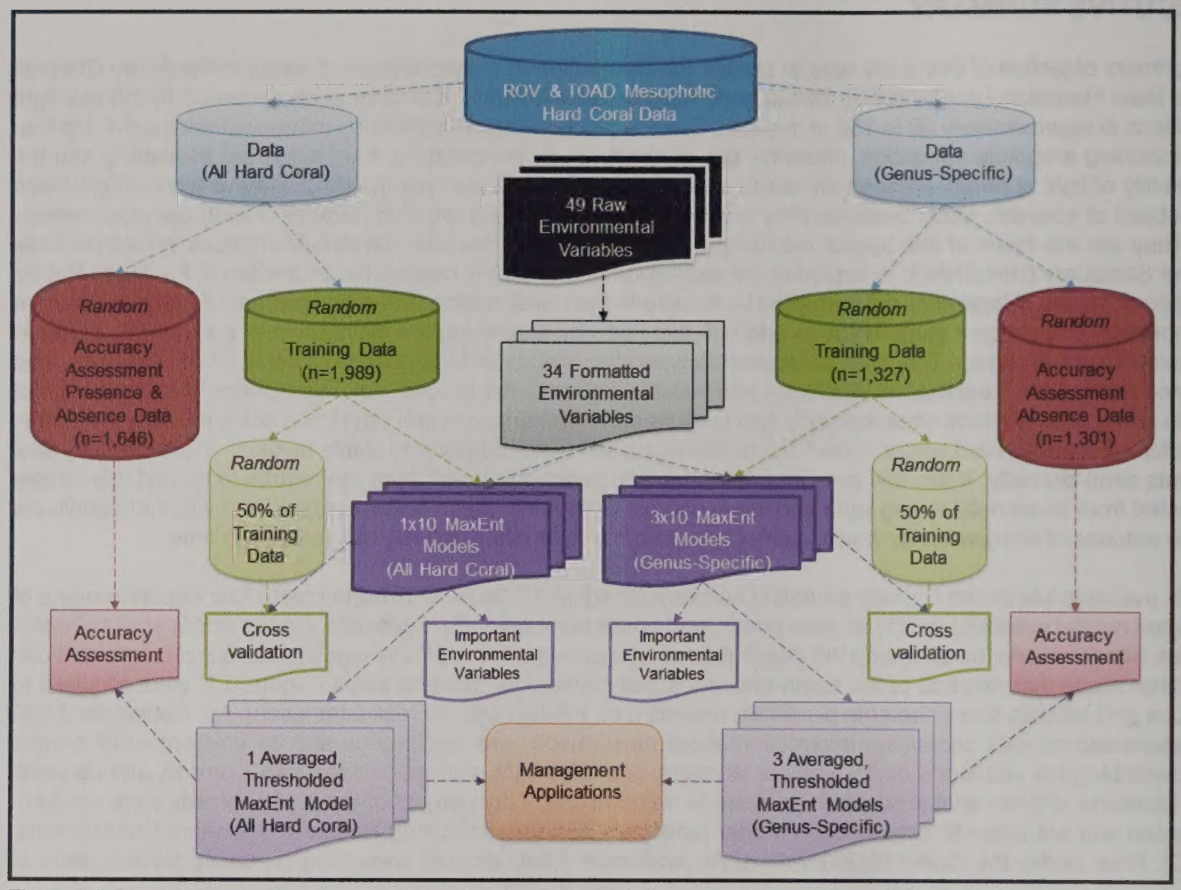

Figure 0.1. Diagram showing the steps needed to develop and validate four ensemble models predicting the habitat suitability of all mesophotic hard corals, *Montipora*, *Porites* and *Leptoseris*.

aside to independently assess the predictive accuracy of the four ensemble models. Suitability thresholds for these models (denoting where corals were predicted to be present/absent) were chosen by finding where the maximum number of correctly predicted presence and absence records intersected on each ROC curve. Permutation importance and jackknife analysis were used to quantify the contribution of each environmental variable to the four ensemble models.

The average test AUCs for the all hard coral, *Montipora*, *Porites* and *Leptoseris* models were between 0.90 and 0.97, indicating 'excellent' overall model performance. Habitat suitability thresholds were set to 25%, 15%, 7% and 20% (i.e., the logistic output value x 100%) for the all hard coral, *Montipora*, *Porites* and *Leptoseris* models, respectively. These numbers denote how suitable a location is for mesophotic corals. Predictive accuracies (measured at these suitability thresholds) were 73.1% overall for all hard corals, and using absences only, were 86.1% for *Montipora*, 85.3% for *Porites* and 78.2% for *Leptoseris*. Permutation importance and jackknife analysis revealed that several environmental variables were important to all four of the ensemble models. These variables included depth, distance from shore, mean euphotic depth, and variance of euphotic depth. Unlike the other models, seafloor complexity (i.e., slope of slope) was also important to the development of the *Leptoseris* ensemble model. While it is likely that these variables are proxies for other variables, suitable environmental conditions for mesophotic corals were highest in a broad region in the south and eastern half of the Au'au Channel. For all hard corals and *Montipora*, predicted suitable conditions were the highest between Lahaina Roads Basin and Papawai Point. This area is characterized by relatively warmer (at the surface), moderately deep and less turbid waters than elsewhere in the study area, suggesting that these two groups prefer moderately deep waters that remain optically clear and stable through time. For *Porites*, suitable conditions were highest between Hanakaoo Point and Hekili Point. This area is characterized by relatively warmer, slightly shallower and less turbid waters than found in other parts of the study area, suggesting *Porites* prefers shallower waters and can tolerate slightly more turbid waters than either *Montipora*

or all hard corals combined. Lastly for *Leptoseris*, suitable environmental conditions were highest offshore of Hekili Point, which has the deepest and most consistently warm and clear waters compared to any other part of the study area. These trends suggest that *Leptoseris* prefers slightly deeper, substantially less turbid and less variable waters (in terms of turbidity) than *Montipora*, *Porites* and all hard corals combined.

Results from this study can be used for a number of management applications, including identifying large areas of high suitability by coral genus; delineating subzones within the sanctuary if special regulations are needed to protect MCEs; and targeting and promoting research and educational activities about these important and rare habitats. These predictive maps may also be overlaid with additional spatial information (e.g., human activities) to evaluate options for minimizing conflicts in areas with many overlapping resources and uses. However before each application, extreme care should be taken when selecting a habitat suitability threshold because it affects the probability of correctly identifying the presence and absence of mesophotic corals. In some cases, it may be more important to correctly identify locations of mesophotic coral presence (e.g., research), while in others, it may be more important to correctly identify absences (e.g., undersea cable routing).

While these models help to fill some knowledge gaps about the distribution of MCEs in the Au'au Channel Region, several data and informational gaps still exist and need to be addressed in the future. These gaps are not unique to the Au'au Channel, as similar gaps exist across the MHI as a whole. To fill some of these gaps, future efforts should focus on developing a systematic sampling plan for mesophotic corals around each of the MHI. Systematic sampling would allow this or similar approaches to be applied to other areas in the MHI, supporting the marine spatial planning needs of the broader ocean community. Establishing a baseline for MCE distributions in the MHI is also critical because it will allow scientists and resource managers to better understand how MCEs are responding to local environmental variations and global climate changes in the future.

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TABLE OF CONTENTS

EXECUTIVE SUMMARY iii

CHAPTER 1: INTRODUCTION 1
1.1. What are mesophotic corals? 1
1.2. Why is HIHWNMS interested in mesophotic corals? 1
Literature cited 3

CHAPTER 2: METHODS 5
2.1. Study Area 5
2.2. Maximum Entropy Modeling 6
2.3. Response Variables (Mesophotic Hard Coral Data) 8
2.4. Predictor Variables (Environmental Data) 9
2.5. Model Development 13
2.6. Model Evaluation 14
Literature Cited 17

CHAPTER 3: RESULTS 21
3.1. All Mesophotic Corals 21
3.2. *Montipora* 25
3.3. *Porites* 27
3.4. *Leptoseris* 29
3.5. Comparisons among Genera 32
Literature Cited 34

CHAPTER 4: DISCUSSION AND CONCLUSION 35
4.1. Discussion 35
4.2. Management Applications 39
4.3. Data and Informational Gaps 40
4.4. Conclusion 42
Literature Cited 43

APPENDIX A: RAW MAXENT OUTPUT (*TO OBTAIN A COPY PLEASE CONTACT LEAD AUTHOR)*

List of Tables

Table 2.1. Records collected by the PIFSC CRED, HURL, the Bishop Museum, DAR and UH, and classified by the PIFSC CRED were used to train or validate the mesophotic hard coral predictions developed using MaxEnt. 9
Table 2.2. Several predictors were used to model the distribution of mesophotic hard corals. These predictors described the seafloor's depth, vertical structure, available light, surface temperature, currents and distance from shoreline. 11
Table 2.3. Parameters used to develop 10x10 m surfaces for euphotic depth and sea surface temperature using ordinary kriging. 12
Table 3.1. Two methods were used to describe predictive performance and accuracy of the MaxEnt models. 21
Table 3.2. Important variables for each model as measured by permutation. 23

List of Figures

Figure 0.1. Diagram showing the steps needed to develop and validate four ensemble models predicting the habitat suitability of all mesophotic hard corals, *Montipora*, *Porites* and *Leptoseris*. iv
Figure 1.1. The "Au'au Channel Region," which includes the Au'au Channel as well as parts of the Kealaikahiki, Alalākeiki, Pailolo and Kalohi Channels. 1
Figure 2.1. Environmental conditions (e.g., wind, waves, rainfall) in the Au'au Channel Region vary widely both in space and time. 5
Figure 2.2. MaxEnt 3.3.3e software was used to develop predictive models of mesophotic hard coral distributions. 6
Figure 2.3. Comparison of MaxEnt to other modeling methods. 7
Figure 2.4. Map of locations of TOAD and ROV points describing the presence and absence of mesophotic hard corals in the Au'au Channel Region and a photo of MCE dominated by colonies of *Leptoseris hawaiiensis* at a depth of 90 m in the Au'au Channel. 8
Figure 2.5. Thirty four predictor variables were included in the MaxEnt modeling process. 12
Figure 2.6. All of MaxEnt input parameters were left at their default values during the modeling process. 13
Figure 2.7. ROC curve showing how a model performs relative to chance. 14
Figure 2.8. Location of spatially independent accuracy assessment points in Au'au Channel Region. 15
Figure 3.1. Proportion of accuracy assessment sites correctly predicted as having hard corals present and absent as a function of MaxEnt habitat suitability value chosen to denote coral presence. 21
Figure 3.2. **a)** Predicted distribution of hard mesophotic coral habitat by suitability values and b) proportion of the study area by suitability values for all hard corals. 22
Figure 3.3. Important variables in the all hard coral model as measured by jackknife of AUC. 24
Figure 3.4. Response curves for environmental variables important to the all hard coral habitat prediction. 24
Figure 3.5. **a)** Predicted distribution of *Montipora* habitat by suitability values and b) proportion of the study area by suitability value for *Montipora*. 25
Figure 3.6. Important variables in *Montipora* model as measured by jackknife of AUC. 26
Figure 3.7. Response curves for environmental variables important to *Montipora* prediction. 26
Figure 3.8. **a)** Predicted distribution of *Porites* habitat by suitability values and b) proportion of the study area by suitability value for *Porites*. 27
Figure 3.9. Important variables in *Porites* model as measured by jackknife of AUC. 28
Figure 3.10. Response curves for environmental variables important to *Porites* prediction. 28
Figure 3.11. **a)** Predicted distribution of *Leptoseris* habitat by suitability values and b) proportion of the study area by suitability value for *Leptoseris*. 29
Figure 3.12. Important variables in *Leptoseris* model as measured by jackknife of AUC. 30
Figure 3.13. Response curves for environmental variables important to *Leptoseris* prediction. 30
Figure 3.14. Overlay of the *Leptoseris*, *Montipora*, and *Porites* single-variable MaxEnt response curves for the variables: a) mean depth, b) distance from shore, c) mean euphotic depth, and d) standard deviation of euphotic depth. 32
Figure 3.15. Predicted distribution of suitable habitat (based on MCSS) for *Porites*, *Leptoseris*, and *Montipora*. 33
Figure 4.1. Four full-water column temperature measurements taken on November 28, 2001 in the middle of the Au'au Channel between Maui and Lanai. 35
Figure 4.2. The dependence of maximum predicted suitability values on the four most important predictors for all four models. 36

CHAPTER 1: INTRODUCTION

1.1. WHAT ARE MESOPHOTIC CORALS?

Researchers have classified coral reef ecosystems into three general depth zones based on species composition and environmental conditions: 1) shallow (~0-30 m deep), sunlight-dependent corals with symbiotic algae (zooxanthellae), 2) mesophotic (~30-150 m) corals still dependent on sunlight but adapted to low light conditions, and 3) deep coral ecosystems (deeper than 150 m) comprised of species lacking zooxanthellae (Hinderstein et al. 2010, Roberts et al. 2009). Mesophotic corals can show a range of adaptations which allow them to live in low light environments including flattened morphologies, pigment specialization, increased heterotrophy, and lower metabolic demands (Kahng et al. 2010). In the Hawaiian archipelago, Kahng and Kelley (2007) and Rooney et al. (2010) found that different types of mesophotic coral ecosystems (MCE) dominated specific depth ranges. In 30 to 50 m of water, upper MCEs were dominated by a low diversity of hard corals found in shallower reefs (*Pocillopora meandrina*, *Pocillopora damicornis*, *Montipora capitata*, and *Porites lobata*). In 50 to 80 m of water, branching/plate coral MCEs were dominated by hard corals with a singular morphology. At 80 to 130 m depths, MCEs were dominated by the coral species, *Leptoseris hawaiiensis*.

Figure 1.1. The "Au'au Channel Region," which includes the Au'au Channel as well as parts of the Kealaikahiki, Alalākeiki, Pailolo and Kalohi Channels. MaxEnt models of mesophotic coral habitat suitability were developed for the study area outlined by the dotted black line.

Several physical factors are assumed to influence the distribution of these MCEs, including aragonite saturation, alkalinity, pH, currents, water temperature, hard substrate availability and the availability of photosynthetically active radiation (PAR) at depth (Grigg 1965, Fricke et al. 1987, Ohlhorst and Liddell 1988, Falkowski et al. 1990, Kahng and Kelley 2007, Kahng et al. 2010, Rooney et al. 2010). Additional research is needed to better understand these mesophotic communities (Kahng and Maragos 2006), as they are increasingly threatened by numerous anthropogenic stressors (Wilkinson 1999, Klyepas and Eakin 2007). Around Hawai'i and elsewhere that reefs occur, the vast majority of coral reef studies have been conducted on shallow reef systems due to accessibility with standard scuba gear (Menza et al. 2008). Unlike most regions, there have also been a number of studies on the deeper reefs in Hawai'i due to the jewelry industry based on black corals (Grigg 1965, 2001, Kahng and Grigg 2005). Mesophotic coral ecosystems have increasingly been the subject of scientific study and are the focus of this spatial modeling effort and assessment to support the Hawaiian Islands Humpback Whale National Marine Sanctuary (HIHWNMS).

1.2. WHY IS HIHWNMS INTERESTED IN MESOPHOTIC CORALS?

The Hawaiian Islands Humpback Whale National Marine Sanctuary was created in 1992 to protect the North Pacific Humpback Whale (*Megaptera novaeangliae*) and their calving and breeding habitat (Oceans Act 1992, NMSP 2002, Calambokidis et al. 2008). The sanctuary is spread across several of the Hawaiian Islands (Figure 1.1) and encompasses many of the insular shelf areas where humpback whales are most frequently sighted (Oceans Act 1992, Craig et al. 2003). While focused on protecting a single whale species, the multipart sanctuary also encompasses many areas important to a wide range of other fauna including seabirds, turtles, other marine mammals, and coral reef ecosystems.

Sanctuary Vision, Goals, and Objectives from NMSP (2002) Management Plan:

*"**GOAL 7**: Identify and evaluate resources and ecosystems for possible inclusion in the Sanctuary"*

At the time of initial designation and again during the 2002 management plan review process, it was recommended that the sanctuary explore expansion of its scope to include the conservation and management of other components of the ecosystem (Oceans Act 1992, NMSP 2002, HIHWNMS and DAR 2007). The present study addresses this need by examining the distribution of mesophotic corals in the Au'au Channel, an unmapped habitat type in a central region of the sanctuary.

The Au'au Channel is located in the Hawaiian Islands between the islands of Maui, Lanai, Molokai and Kahoolawe. The study region also includes parts of the Kealaikahiki, Alalākeiki and Kalohi Channels between these islands but we will refer to the study area as the "Au'au Channel region" for brevity (Figure 1.1). The channel reaches depths of 140 m, however the majority of the seafloor is in the mesophotic depth range between 40 and 90 m deep. Topography on the channel floor consists of numerous drowned solution basins and ridges, sediment plains, and conical reef pinnacles (Grigg et al. 2002). These were exposed during periods of low sea level during multiple glacial periods over at least the last 800,000 years (Lambeck et al. 2002). Reef growth in the Channel during the Holocene consists of a thin veneer a few meters thick on those topographic highs (Grigg et al. 2002).

The Au'au Channel is a priority region for the HIHWNMS and other researchers for variety of reasons. In addition to being a focus of humpback whale activity in the winter months (Craig et al. 2003), it is also the historical center of the black coral jewelry industry in Hawai'i (Grigg 1965, 1993). This has led to extensive interest in seafloor surveys of coral beds by divers for jewelry production and even harvesting with ROVs and submersibles. More recently, research on the unique geology and reef communities of this region has increased due to the broad area of potentially suitable mesophotic habitat and the recent discovery of some areas with extensive coral coverage and *Halimeda* beds at mesophotic depths (Grigg et al. 2002, Kahng and Grigg 2005, Kahng and Kelley 2007, Rooney et al. 2010).

Objectives of this study were to: 1) identify a relatively simple, low-cost and robust modeling approach to predict mesophotic coral distribution based on available data, 2) create a spatially explicit predictive model for mesophotic coral occurrence in the Au'au channel and surrounding region of the HIHWNMS, and 3) train the sanctuary staff in use of the approach to enable similar studies in other areas as additional data become available. Other reef types and bottom features, including azooxanthellate and shallow reef assemblages, were beyond the scope of this project.

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2.1. STUDY AREA

The environmental conditions (e.g., wind, waves, rainfall) vary widely in the Au'au Channel region both in space and time (Figure 2.1). Weather conditions throughout the Hawaiian Islands are largely controlled by the seasonal wind and wave patterns as well as the high shield volcanoes on the islands (Fletcher et al. 2008). From October to April, southerly winds (locally referred to as "Kona" winds) occasionally create conditions that result in heavy rainfall events. Large, long-period swells from the north and northwest and short-period swells from the south associated with Kona events are dominant during this period. The northeast trade winds become more persistent from May to October. The short-period southern swells associated with the Kona winds are replaced with longer-period southern swells and short-period northeasterly waves generated by the trade winds. The winter months bring damaging North Pacific swells that may limit coral growth (especially in shallow waters) on the north side of the islands (Grigg 1998). It can also refract around islands and combine with the trade wind waves, creating large, energetic waves that can greatly reduce coral growth on the eastern and western sides of the islands (Fletcher et al. 2008). However, much of the Au'au Channel is protected from these trade wind waves, the North Pacific swell and their refraction around Maui.

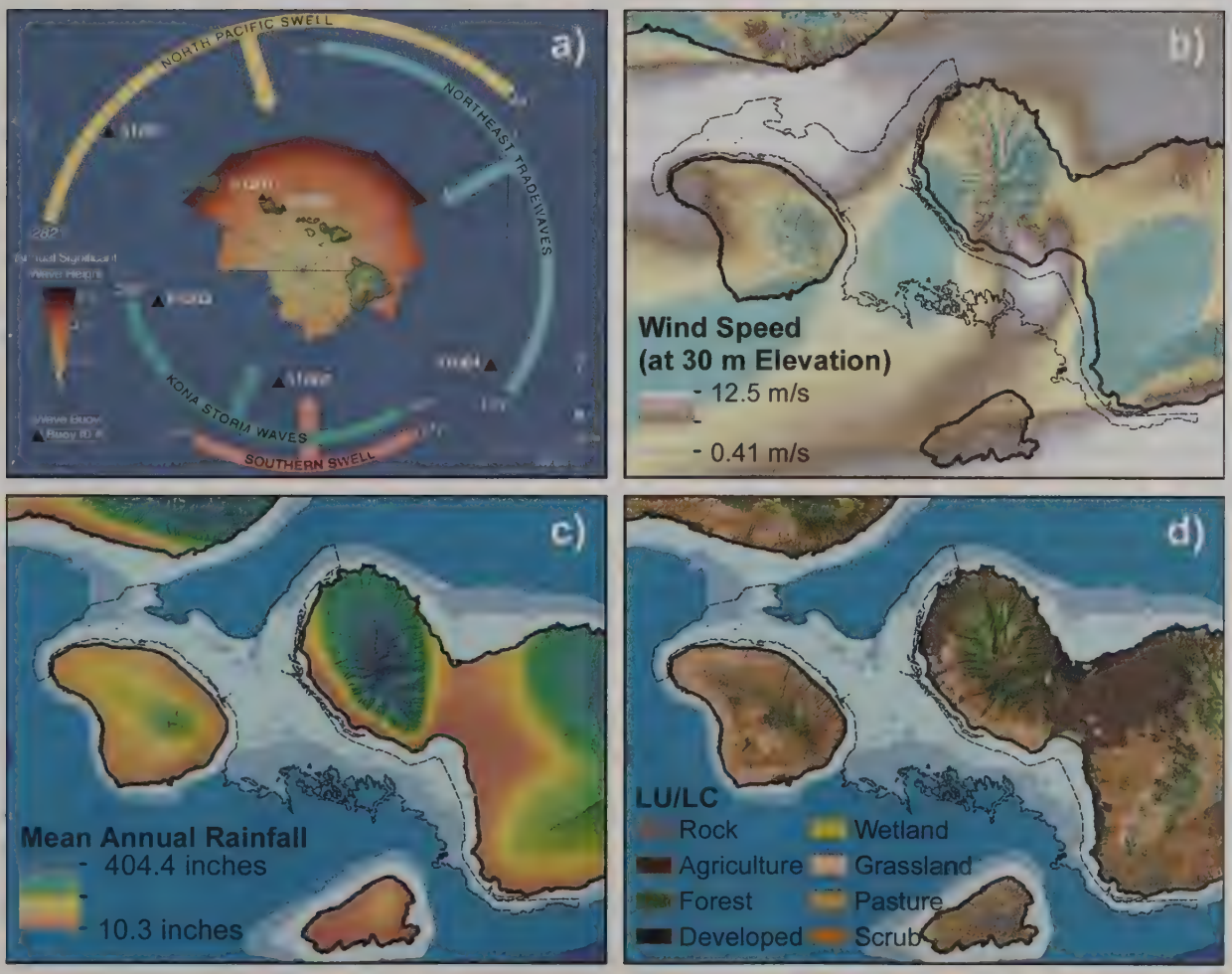

Figure 2.1. Environmental conditions (e.g., wind, waves, rainfall) in the Au'au Channel Region vary widely both in space and time: a) Predominant direction and height of waves during the winter and summer months. Figure reproduced from Fletcher et al. 2008. b) Modeled mean wind speed at 30 m in elevation in the Au'au Channel Region (AWS, 2004). c) Mean annual rainfall from 1978 to 2007 in the Au'au Channel Region (Giambelluca et al. 2011). d) Land use/land cover for Maui, Lanai, Kahoolawe and Molokai from 2005 (NOAA CSC, 2008).

The trade winds deliver moist air to the northeastern sides of the islands (Fletcher et al. 2008). The high shield volcanoes block this moist tropical air, causing it to rise, condense and then fall as heavy rain on the windward sides of the MHI. On Maui in particular, the western mountains act as a shield, creating a pocket of persistently windless (<0.41 meters per second at 30 m in elevation) conditions southeast of the island in the Au'au Channel. This relatively windless area is in stark contrast to north and south parts of the Au'au Channel Region as a whole, which often see winds up to 12.5 meters per second (i.e., 45 kilometers per hour). The western Maui mountains also cause a rain shadow on the island, making the leeward side of Maui much drier than the windward side. In particular, the leeward grasslands on Maui receive on average less than 10 inches of rain annually, while the upland forests can receive over 400 inches.

This precipitation gradient, along with large areas of plowed agricultural land, cause on average more sediment to be discharged into coastal areas in the north part of west Maui (i.e., around Kahana) than in the southern part (i.e., southeast of Lahaina) (Vermeij et al. 2008). Kona storms can precipitate extreme rainfall events, leading to periodic mass erosion events. Much of these fine grained sediments persist in the water column along this northern stretch of coastline, as they are continually resuspended by wave and wind-generated turbulence (Storalazzi et al. 2006). Along the southern coastline, semi-diurnal tidal currents help to flush these suspended sediments out to sea most notably during the spring tides (i.e., new and full moons) (Storlazzi et al. 2004). Mild wind conditions south of western Maui mitigate the resuspension of sediments that are not flushed out by these semi-diurnal tides. Together, these strong tidal currents and slack winds create an area with consistently good water quality and clarity. Lower amounts of agriculture and development (compared to central Maui) also preserve these clear water conditions. Much of the land in the southern part of western Maui (i.e., from Lahaina to McGregor Point) is unsuitable for agriculture (Maui County, 2010), and currently, less than 10% of the watershed in these areas has been developed (Crane, 2011). However, this trend may change with the implementation of the Maui 2030 directed growth plan, which calls for the developed area in these watersheds to double by 2030 (Crane, 2011). It is unclear how these proposed changes will affect sedimentation along the leeward waters of western Maui, although runoff mitigation and watershed restoration measures are likely to be put into place.

2.2. MAXIMUM ENTROPY MODELING

2.2.1. What is Maximum Entropy Modeling?

Freely available Maximum Entropy modeling software (MaxEnt 3.3.3e) was used to create a spatially explicit predictive surface of MCE habitat suitability in the Au'au Channel Region. MaxEnt (Figure 2.2; Phillips et al. 2006; Phillips and Dudík, 2008) is a modeling technique that predicts animal or plant distributions using presence-only data (i.e., data containing records only of locations where the animal or plant was present). MaxEnt makes these predictions by analyzing the distribution of environmental variables associated with the species' presence (also known as "occurrence") to find other areas that meet all of these environmental constraints (without making any assumptions about what is not known). Statistically speaking, MaxEnt finds the probability distribution of maximum entropy (i.e., the distribution that is the most spread out) and then constrains it using a set of values of environmental variables where the species is known to occur.

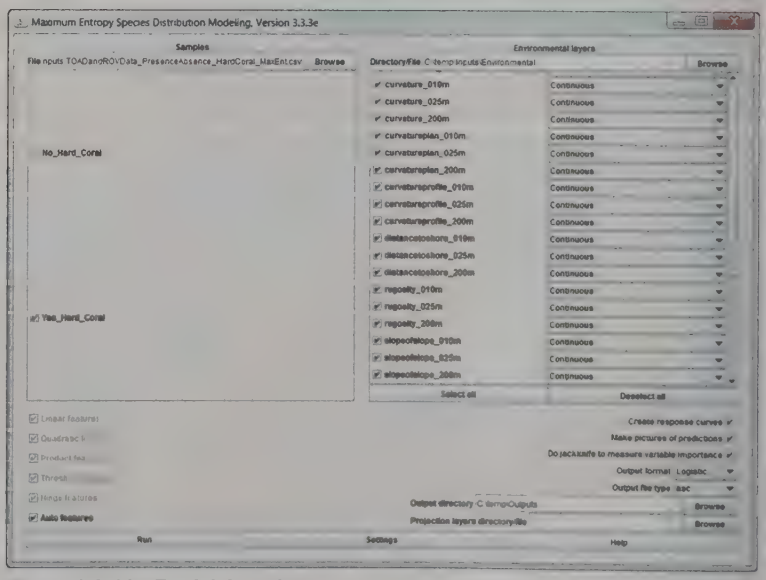

Figure 2.2. MaxEnt 3.3.3e software was used to develop predictive models of mesophotic hard coral distributions. The main graphical user interface screen for the MaxEnt software is shown above.

Like other modeling approaches, MaxEnt is not without its biases and limitations, and can be sensitive to the amount and accuracy of the presence-only data and the ecological relevance and scale of predictor variables (Elith et al. 2011). Presence-only data may be affected by a number of issues, including: (1) the probability of detecting a species at a specific location, (2) sample selection bias and uneven sampling effort, where some areas are more intensively sampled than other areas, (3) spatial autocorrelation of samples, and (4) uncertainties associated with the temporal and/or spatial scale of the sample data (Phillips et al. 2006; Elith et al. 2011). However, almost all of these issues are problematic for presence-absence datasets and modeling techniques as well (Fielding and Bell 1997; Manel et al. 2001; Hirzel and Guisan 2002; Dormann et al. 2007). In particular, sample selection bias affects presence-absence models because it influences the spatial autocorrelation of the dataset and the prevalence (i.e., frequency of occurrence) of the organism. Thus, spatial autocorrelation and prevalence values will differ depending on how samples were collected, which is problematic because these values affect the significance (Fielding and Bell 1997) and magnitude (Manel et al. 2001) of model accuracy statistics, respectively. In addition to prevalence and autocorrelation, it has been suggested that unreliable absence records (due to a variety of factors, including inadequate survey effort) may give presence-only datasets an advantage over presence-absence datasets (Jiménez-Valverde et al. 2008; Lobo et al. 2010).

2.2.2. Why was MaxEnt used to model mesophotic coral distributions?

The MaxEnt approach to spatial modeling compares favorably to other modeling techniques including generalized linear models (GLM), generalized additive models (GAM), boosted regression trees (BRT), genetic algorithm for rule-set prediction (GARP) and environmental niche factor analysis (ENFA) (Figure 2.3; Elith et al. 2006; Hernandez et al. 2006; Phillips et al. 2006; Pearson et al. 2007; Tittensor et al. 2009; Pittman and Brown 2011). For this study, MaxEnt was chosen over these other modeling approaches for several reasons. First, the HIHWNMS would like to use this modeling approach to predict the distribution of hard mesophotic corals over a larger geographic area within the Sanctuary, and eventually throughout the Main Hawaiian islands. However, data describing the distribution and abundance of mesophotic hard corals is sparse in the MHI. If this modeling approach is to be expanded in the future, it will require that mesophotic coral data be compiled from various platforms of opportunity. It is likely that the majority of this opportunistic data will be presence-only (or diverse datasets that will need to be standardized to presence only), making MaxEnt a more broadly applicable approach and a more likely candidate for future modeling efforts.

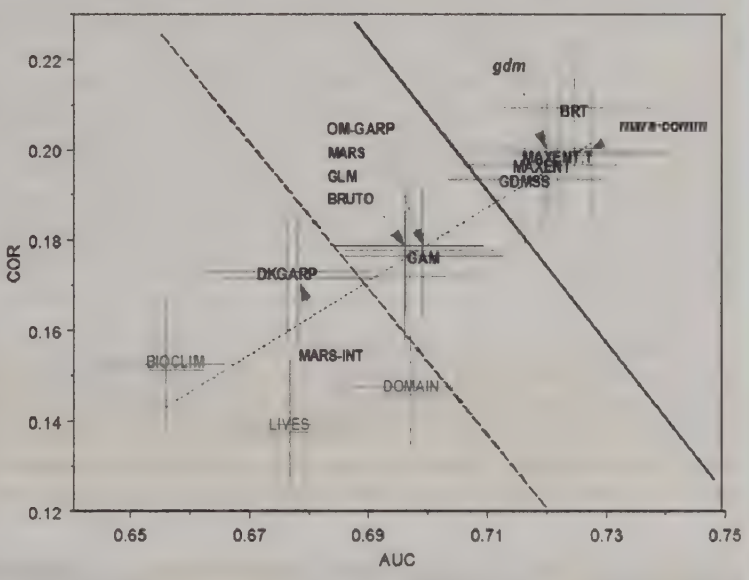

Figure 2.3. Comparison of MaxEnt to other modeling methods. This figure depicts the mean area under the curve (AUC) versus mean correlation (COR) values for several species distribution modeling methods. MaxEnt outperformed many of these modeling methods, including generalized linear models (GLMs) and generalized additive models (GAMs). Figure adapted from Elith et al. 2006.

The second reason that MaxEnt was chosen over other approaches was because it is simpler to understand, more flexible and easier to apply than some of the other modeling techniques available. MaxEnt models are based on easily formatted, raster inputs, produced using simple menus in a graphic user interface, and yield results including maps and figures in preformatted, publication-quality outputs. Simplicity is important during model development for staff that may not have the statistical background, specialized software, or time to engage in more complex and time consuming approaches. Simplicity is also important when trying to deconstruct and understand how each environmental variable influences habitat suitability and what variables are important for predicting a species distribution. MaxEnt uses several different approaches to tease apart the contribution of each environmental variable to the overall prediction. A simpler model may also be easier to transfer and apply to

other areas in the MHI, although care must be taken in doing so (Elith et al. 2011). In addition to being a simpler approach, MaxEnt is also a flexible approach because it can utilize both continuous and categorical predictor data, is fairly robust to correlated environmental predictors (Wollan et al. 2008) and can incorporate interactions among predictor datasets (Phillips et al. 2006). Such flexibility is important if the ecological niche of a species is poorly defined or understood. It also reduces (but does not negate) the need to choose uncorrelated predictors that may be ecologically relevant to a species' local distribution (Elith et al. 2010).

The third reason that MaxEnt was chosen over other techniques was because it compared favorably, in terms of predictive performance and accuracy, to other modeling techniques (Elith et al. 2006; Hernandez et al. 2006; Phillips et al. 2006; Pearson et al. 2007; Tittensor et al. 2009; Pittman and Brown 2011). One measure of the predictive accuracy of a model is the number of independent samples correctly predicted divided by the total number of samples. For example, a model would have an overall accuracy of 80% if 1,200 out of 1,500 samples were correctly predicted. For other applications, we might be concerned not just with overall model accuracy, but also with model performance, which is defined as the ratio of true positive predictions to false positive predictions. Models that perform well have higher true positive prediction rates than false positive prediction rates. If a model performed no better than random chance, its true and false positive prediction rates would be equal. Applying these metrics of model accuracy and performance, Elith et al. 2006 found that MaxEnt was in the highest reforming group in terms of AUC (area under the curve), correlation and Cohen's kappa when predicting the distribution of terrestrial species in several locations around the world. Given that the primary goal of this project is to produce the most accurate prediction of mesophotic hard coral distributions possible, the results of Elith et al. 2006 suggest that MaxEnt is capable of producing spatial predictions that are (at the very least) as accurate as some of the more complicated and labor intensive modeling techniques available. To test this trend and evaluate the predictive accuracy of MaxEnt, 10 models were fit to different, randomly selected subsets of 50% of the data. The final reported model predictions are averages of these 10 replicates. Moreover, a randomly chosen 30% of the mesophotic hard coral absence and presence data were set aside at the beginning and used to independently assess the accuracy of MaxEnt predictions. This accuracy assessment is discussed in more detail in Section 2.6.2.

2.3. RESPONSE VARIABLES (MESOPHOTIC HARD CORAL DATA)

The response variable for this project was the presence of mesophotic hard corals (Figure 2.4). Observations were compiled from underwater video and photos collected in the Au'au Channel region during fourteen research missions from November 25, 2001 to September 26, 2011. These research missions were funded by NOAA's Office of Marine Aviation Operations and NOAA's Center for Sponsored Coastal Ocean Research (CSCOR). They were led by the Bishop Museum, the Hawaii Division of Aquatic Resources, PIFSC and the University of Hawaii,

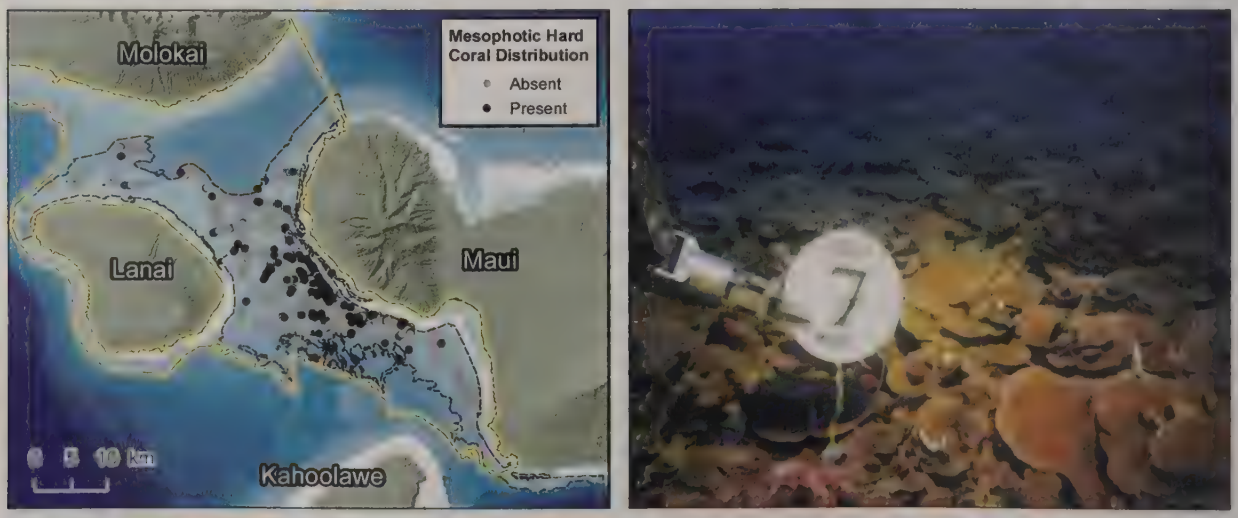

Figure 2.4. Location of TOAD and ROV points describing the presence and absence of mesophotic hard corals in the Au'au Channel Region (left). MCE dominated by colonies of *Leptoseris hawaiiensis* at a depth of 90 m in the Au'au Channel (right). Photo adapted from Rooney et al. 2010. Photo credit: Hawai'i Undersea Research Laboratory.

and some of the cruises were done in collaboration with the Hawaii Undersea Research Laboratory. Two pieces of equipment and several platforms were used to acquire this large collection of georeferenced underwater video and photographs. Specifically, a Towed Optical Assessment Device (TOAD) camera sled was deployed in 2008 to 2011 aboard the NOAA ships Oscar Elton Sette and Hi'ialakai, and a RCV-150 Remotely Operated Vehicle (ROV) was deployed in 2001, 2002, 2004 and 2006 to 2011 aboard HURL's R/V Ka'imikai-o-Kanaloa. The positional uncertainty associated with the camera sled and ROV video ranges from ± 15 to 100 m. Please see PIFSC 2008 and Rooney et al. 2010 for more information about these cruises and for more details about the TOAD and ROV systems. Video data from camera sled and ROV dives were compiled and classified by CRED every 30 seconds at 5 points spaced equidistantly in a horizontal line across the monitor screen. Substrate type, living biological cover (including hard coral, crustose coralline algae, macroalgae and soft corals) and other benthic characteristics were recorded in the classification process. The quality of the video prevented classification to the species level in some locations. For more information about this classification scheme and method, please see the following websites (ftp.soest.hawaii.edu/pibhmc/website/webdocs/webtext&figures/bh_class_codes.htm and ftp.soest.hawaii.edu/pibhmc/website/webdocs/documentation/Optical-Proc-Overview.pdf).

From these fourteen research missions, 22,843 georeferenced records were classified using CRED's protocol and classification scheme (Table 2.1). These classified records were provided by CRED on February 29, 2012 in three separate excel tables. Edits made by CRED to these classified records after this date were not included in this modeling effort. These excel tables were converted to shapefiles, merged together, and projected into a common coordinate system (i.e., NAD 83 UTM 4 N). Each record was then converted from abundance values to presence-absence values (i.e., 0 = absent and 1 = present). After this conversion, close to 5,550 records were selected and removed from further analysis because they fell outside the Au'au Channel study area and/or outside the temporal range (2004 to 2010) of some of the environmental predictors (i.e., euphotic depth and sea surface temperature). Seventy percent (n= 1,989) of the remaining 2,841 presence records were randomly chosen and used to develop a MaxEnt model predicting the distribution of all mesophotic hard corals in the Au'au Channel Region. Thirty percent of the presence and absence data (n=852 and n= 4,332, respectively) were set aside to evaluate this models' predictive accuracy. This same absence data was also used to analyze the commission errors of the genus-specific models. To develop genus-specific distribution models, points that contained presence information about multiple coral genera (148 in all) were split into separate records. Subsequently, an additional 1,514 points were removed from analysis because they were unclassified or because there were not enough presence records (<100) to develop a reliable spatial prediction for a specific coral genus (i.e., *Pocillopora* and *Other*). This deletion left 1,327 points, which were used to develop genus-specific coral distribution models for *Leptoseris*, *Montipora* and *Porites*.

Table 2.1. Records collected by the PIFSC CRED, HURL, the Bishop Museum, DAR and UH, and classified by the PIFSC CRED were used to train or validate the mesophotic hard coral predictions developed using MaxEnt.

GROUP	# OF RECORDS	# OF RECORDS USED TO DEVELOP MODELS	# OF RECORDS USED TO VALIDATE MODELS
Hard Corals Present	2,841	(2,841*0.7) = 1,989	(2,841*0.3) - 507 = 345
Leptoseris	617	617	-
Montipora	605	605	-
Other Corals	62	-	-
Pocillopora	11	-	-
Porites	105	105	-
Unclassified	1,441	-	-
No Hard Corals Present	14,441	-	(14,441 * 0.3) - 3,031 = 1,301
Sub Total	17,282		
Outside study area	2,061		
Outside temporal period	3,500		
Total	22,843	1,989	1,646

2.4. PREDICTOR VARIABLES (ENVIRONMENTAL DATA)

Several physical factors are thought to influence the distribution of MCEs, including water temperature, currents, hard substrate complexity and availability, water chemistry (i.e., aragonite saturation) and the availability of PAR at depth (Leclercq et al., 2000; Guinotte et al., 2006; Kahng and Kelley, 2007; Tittensor et al. 2009; Rooney et al. 2010). Given their potential importance, many of these physical factors were included in this mesophotic coral modeling effort as predictor variables. Table 2.2 describes each of the predictor variables that were evaluated for inclusion in this study. Information about water chemistry, water temperature at depth and variation in cloud cover were not included because data for these variables were not readily available for the time period (2004 to 2010) and/or geographic area (Au'au Channel Region) examined here. The 21 raw predictors that were included were compiled from a variety of sources, including the University of Hawaii (UH) School of Ocean and Earth Science and Technology (SOEST) (Carter et al. 2008; Hafner, 2005; Carter and Potemra, 2012; UH SOEST, 2012), the National Aeronautics and Space Administration (NASA) (NASA, 2012) and the U.S. Geological Survey (USGS) (Gardner et al. 1998).

Additional processing steps were needed before spatial models of mesophotic corals could be developed using these predictor surfaces. The primary purpose of these steps was to standardize the: (1) geographic extent, (2) format, (3) coordinate system, and (4) in some cases, the spatial resolution of the different images. These steps improved the consistency of the predictors' georeferenced location, making it less likely that the process of model development would be negatively impacted by spatial uncertainty associated with the predictors. The first step in this process was to transform each predictor to the same coordinates system (i.e., NAD83 UTM 4 North). Each predictor was clipped to the same geographic extent, snapped to the 10x10 m bathymetry surface, and saved to an ESRI ASCII (.asc) file. The ESRI ASCII format was used because it can be easily ingested by the MaxEnt software package. Using the environment settings, predictors were snapped to the 10x10 m bathymetry surface because this surface had the finest spatial resolution and presumably, the least amount of spatial uncertainty associated with it (Gardner et al. 1998).

Eleven metrics describing the complexity (i.e., vertical structure) of the seafloor were calculated from the 10x10 m bathymetry surface using several tools in ArcGIS's Benthic Terrain Modeler (Wright et al. 2005), DEM Surface Toolbox (Jenness, 2011) and ArcGIS's Spatial Analyst Toolbox (Table 2.2). Spatial Analyst Toolbox was also used to calculate the geographic distance of each grid cell in the Au'au Channel Region to the closest shoreline. All of these metrics were chosen based on previous studies that suggested they were potentially influential predictors of hard coral presence (Dolan et al. 2008; Pittman et al. 2009; Woodby et al. 2009). The mean of these complexity metrics were also computed at two additional spatial scales (i.e., inside circles with radii of 25 and 200 m). Predictors at these different scales were included to explore the influence of spatial scale on MaxEnt's predictive performance. Since the spatial scale of the oceanographic variables (i.e., light availability, sea surface temperature and tidal currents) did not match those of the complexity and geographic metrics, several more steps were required before they could be included in the model.

To match the spatial resolution of the other predictor surfaces, the tidal current surfaces were resampled from 1x1 km to 10x10 m using cubic convolution. As cubic convolution is not an interpolation method, the purpose of this step was to make the spatial resolutions of tidal current surfaces and the other predictors the same. Grand mean, minimum, maximum and standard deviation were calculated from 2004 to 2010 annual mean euphotic depth surfaces (i.e., PAR availability) and sea surface temperature surfaces (SST). These grid surfaces were converted to points, and ordinary kriging was used to develop geostatistical predictions at 10x10 m. Table 2.3 describes the default parameters used to develop these predictions, and the cross validation root-mean-square errors of the kriged surfaces. Kriging was used (instead of resampling) to change the spatial resolutions of the SST and light availability predictors because several data gaps existed and needed to be filled around the islands of Maui, Lanai, Kahoolawe and Molokai. With the addition of these kriged oceanographic surfaces, a total of 49 predictors were considered for inclusion in the MaxEnt modeling process. The correlation of these 49 predictors was explored at 30 spatially independent locations using Spearman's Rank tests. These 30 points were selected by creating and analyzing ten regularly-spaced point grids between 500 and 5,000 m using a global Moran's I test in ArcGIS's SA Extension. Even though MaxEnt is fairly robust in dealing with correlated predictors, 15 predictors were removed from further analysis that were significantly ($p \leq 0.05$) and highly correlated (>0.85) with other predictors to reduce the amount of computational time needed to create a model. Predictors calculated at coarser spatial scales (i.e., 25 x 25 and 200 x 200 m) were an exception to this rule, as they were often significantly and highly correlated with their finer and/or coarser scale counter parts. These predictors were left in the analysis to explore the influence of spatial scale on MaxEnt's predictive performance. The remaining 34 predictors (Figure 2.5) were included in the spatial modeling of mesophotic hard coral presence in the Au'au Channel Region.

Table 2.2. Several predictors were used to model the distribution of mesophotic hard corals. These predictors described the seafloor's depth, vertical structure, available light, surface temperature, currents and distance from shoreline.

Variable	Data Description	Variable	Units	Definition	Spatial Resolution	Temporal Resolution	Data Source	# Predictors	Predictors Used to Develop Models
Response	Hard coral presence	123 classified video transects (6,081 ROV + 11,201TOAD = 17,282 points)	N/A	Presence/absence of hard corals (by genus) between 30 and 150 m in depth. Spatial uncertainty = ± 15 to 100 m	Mean nearest neighbor distance of points =13 m; Mean height above seafloor unknown	09/09/2004 – 07/17/2010	PIFSC CRED, HURL, Bishop Museum, DAR and UH, 2012	-	-
Predictor (Environmental)	Seafloor Complexity	Aspect	Degrees	Compass direction of maximum slope calculated using ArcGIS's Aspect tool.	10x10, 25x25* and 200x200 m*	N/A	USGS (Gardner et al. 1998); UH SOEST, 2012; PIFSC CRED 2008	11 x 3 = 33	Aspect, Bathymetry, BPI, Curvature (General, Plan & Profile), Rugosity and Slope of Slope at 10x10, 25x25, 200x200 m
		Depth	Meters	Depth of seafloor.					
		Depth (Mean)	Meters	Average water depth calculated using ArcGIS's Focal Statistic tool.					
		Depth (Stdev)	Meters	Dispersion of water depth around the mean calculated using ArcGIS's Focal Statistic tool.					
		Bathymetric Position Index (BPI)	Unitless - = concave + = convex	Measure of where a reference location is (vertically) compared to locations surrounding it. BPI was calculated using the Benthic Terrain Modeler (Wright et al. 2005)					
		Curvature (General)	1/100 meters - = concave + = convex	Measure of convexity/concavity of the landscape calculated using ArcGIS's Curvature tool.					
		Curvature (Plan/Cross-sectional)		Curvature of the surface perpendicular to the maximum slope direction calculated using ArcGIS's Curvature tool.					
		Curvature (Profile/Longitudinal)		Curvature of the surface paralell to the maximum slope direction calculated using ArcGIS's Curvature tool.					
		Rugosity	Unitless	Ratio of surface area to planar area calculated using DEM Surface Tools (Jenness, 2011).					
		Slope	Degrees	Maximum rate of change in slope calculated using ArcGIS's Slope tool.					
		Slope of Slope*	Degrees of Degrees	Maximum rate of maximum slope change calculated using ArcGIS's Slope tool.					
	Light Availability	Euphotic Depth Zone	Meters	Depth of the euphotic zone derived using the Morel model (Morel et al. 2007) The euphotic zone is defined as the area where photosynthetically active radiation (PAR) levels are > 1% of surface levels. PAR is the spectral range of sunlight (400-700 nm) that organisms can use in the process of photosynthesis.	4x4 km (Krigged 10x10 m)	2004 - 2010 (Grand mean, minimum, maximum, standard deviation)	NASA, 2012	4	Grand mean & standard deviation
		Variation in cloud cover	N/A	Persistent cloud cover in Main Hawaiian Islands binned every 12 hours.	1x1 km	11/2004 – 1/2005	UH APDRC (Hafner, 2005)	-	-
	Water Temperature	Sea Surface Temperature (SST)	Degrees Celsius	Temperature of the sea surface during the daytime as measured by MODIS Aqua sensor.	4x4 km (Krigged to 10x10 m)	2004 - 2010 (Grand mean, minimum, standard deviation)	NASA, 2012	3	Grand mean & standard deviation
		Temperature at depth	Degrees Celsius	In situ temperture of water column.	N/A	Unknown	NOAA NODC, 2012	-	-
	Currents	Modeled tidal current velocity at depth	Centimeters/ Second	Tidal current velocities (based on seasonal mean water stratification) modeled hourly and averaged over one year.	1x1 km at 35 & 85 m depths (Resampled to10x10 m)	Annual mean, maximum, variation in speed	UH APDRC (Carter and Potemra, 2012; Carter et al. 2008)	3 x 2 = 6	Mean (35 & 85 m), variation (35 m)
	Water Chemistry	pH	Unitless	The acidity/basicity of sea water. pH < 7 is acidic and pH values >7 are basic or alkaline.	N/A	Unknown	NOAA NODC, 2012	-	-
		Aragonite saturation	µmol/kg	The availability of aragonite (calcium carbonate) in sea water.	N/A	Unknown			
		Alkalinity	µmol/kg	The capacity of sea water for neutralizing an acid solution. Positive values indicate supersaturation and negative values indicate undersaturation.	N/A	Unknown			
	Geographic	Distance to Shoreline	Meters	Distance to shoreline calculated using ArcGIS Euclidean Distance tool.	10x10, 25x25* and 200x200 m*	N/A	GIS Derived	1 x 3 = 3	10x10, 25x25, 200x200 m
						Total # of Predictors		49	34

Table 2.3. Parameters used to develop 10x10 m surfaces for euphotic depth and sea surface temperature using ordinary kriging. These parameters were incrementally changed to minimize the root mean square error of the final surfaces.

VARIABLE	TRANS-FORMATION TO NORMALITY	ORDER OF TREND REMOVAL	SEMIVAR-IOGRAM MODEL	NUGGET	RANGE	ANISOT-ROPY	NEIGBOR-HOOD	# NEIGH-BORS INCLUDED	ROOT MEAN SQUARE ERROR
Euphotic Depth (Mean)	Box-Cox (10)	Constant (60% Local)	Gaussian	0	15,306	29.8°	4 sector with 45° offset	Maximum= 5 Minimum= 2	1.03
Euphotic Depth (Stdev)	Log	Constant (60% Local)	Stable	0	23,348	85.1°	4 sector with 45° offset	Maximum= 5 Minimum= 2	0.53
SST (Mean)	None	Constant (60% Local)	Gaussian	0.002	69,105	89.3°	8 sector	Maximum= 5 Minimum= 2	0.06
SST (Stdev)	Box-Cox (-1)	Constant (60% Local)	Gaussian	0	7,984	0°	4 sector with 45° offset	Maximum= 5 Minimum= 2	0.04

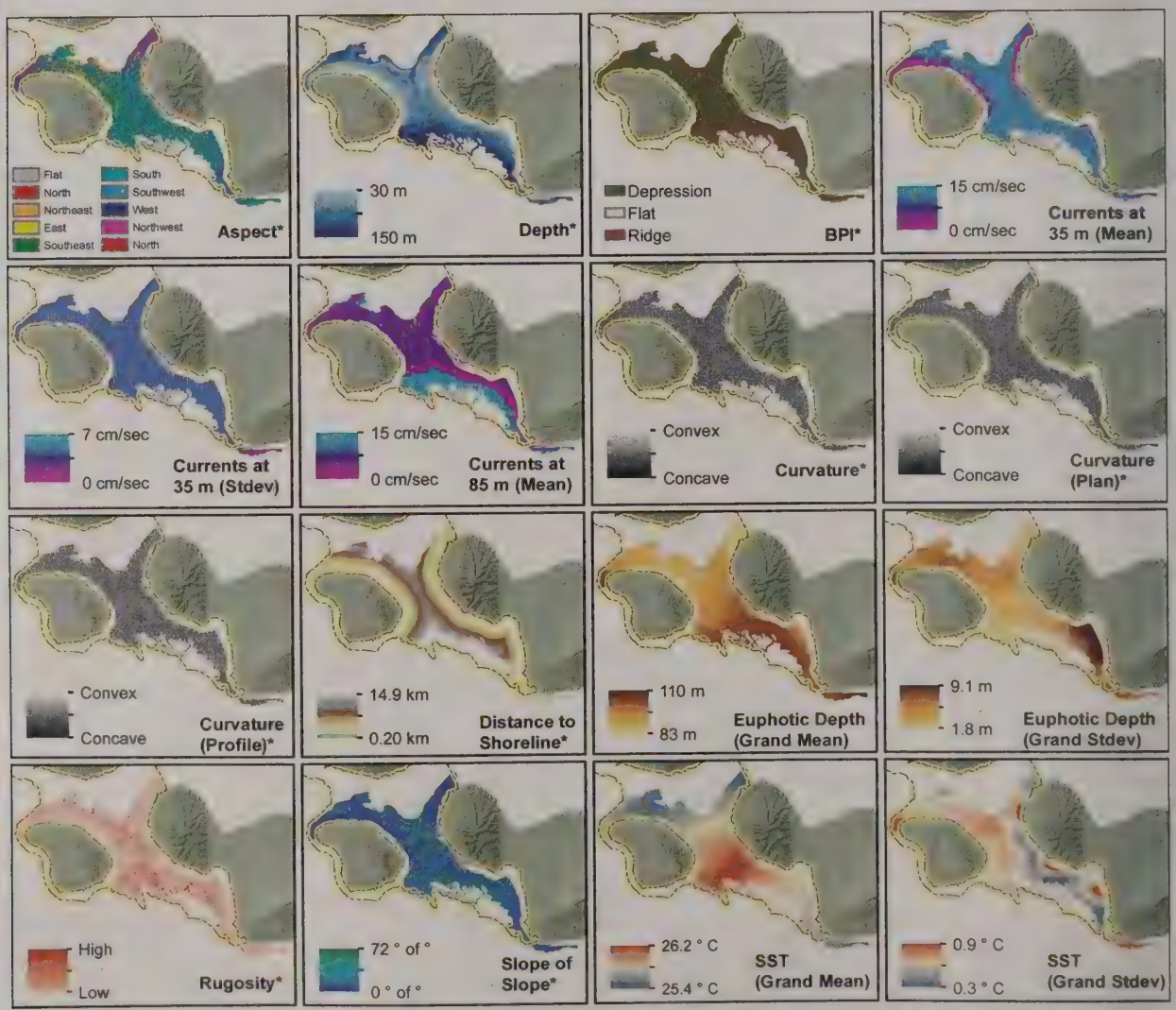

Figure 2.5. Thirty four predictor variables were included in the MaxEnt modeling process. Nine of these variables (denoted by an asterisk) were included at two additional spatial scales (25 x 25 and 200 x 200 m).

2.5. MODEL DEVELOPMENT

Four MaxEnt ensemble models (i.e., aggregate models based on several model replicates fit to random subsamples of the data) were developed for the Au'au Channel Region. One ensemble model predicted the distribution of all hard mesophotic corals, and the remaining ensemble models predicted the distribution of three different coral genera (i.e., *Leptoseris*, *Montipora* and *Porites*). The same 34 predictors were included in, and the same input parameters were used for, all of these predictive models. The majority of the MaxEnt input parameters were left at their default value (Figure 2.6), since few guidelines exist for optimizing these parameters (Phillips et al. 2006), and even fewer exist for optimizing these parameters for modeling mesophotic corals (Tittensor et al. 2009; Howell et al. 2011). The few model parameters that were changed include: Random seed (on), Replicated run = Subsample, Random test percentage = 50, Replicates = 10, Maximum iterations = 1,000 and Regularization = 1. A randomly chosen starting point and subsample of 50% of the data were used to reduce the likelihood of a single point or set of points biasing the overall model results. It was also used to independently assess the predictive performance of these models and to calculate the importance of individual variables. The modeling process was replicated 10 times for each of the four predictive groups (10 x 4 = 40 models total), so that variance could be calculated for each model ensemble. Response curves, spatial predictions and jackknife analysis were developed for each model replicate (Appendix A (contact lead author)), and these results were averaged by predictive group to produce the final MaxEnt performance metrics and spatial predictions for all hard mesophotic corals, *Leptoseris*, *Montipora* and *Porites*. For each model, predicted habitat suitability values ranged logistically from 0 (0% suitable) to 1 (100% suitable). It is important to note that these habitat suitability values are not probabilities and are not necessarily expected to correlate with abundance. They only indicate the relative suitability of a habitat for mesophotic corals, based on the values of environmental variables at other locations where mesophotic corals were observed.

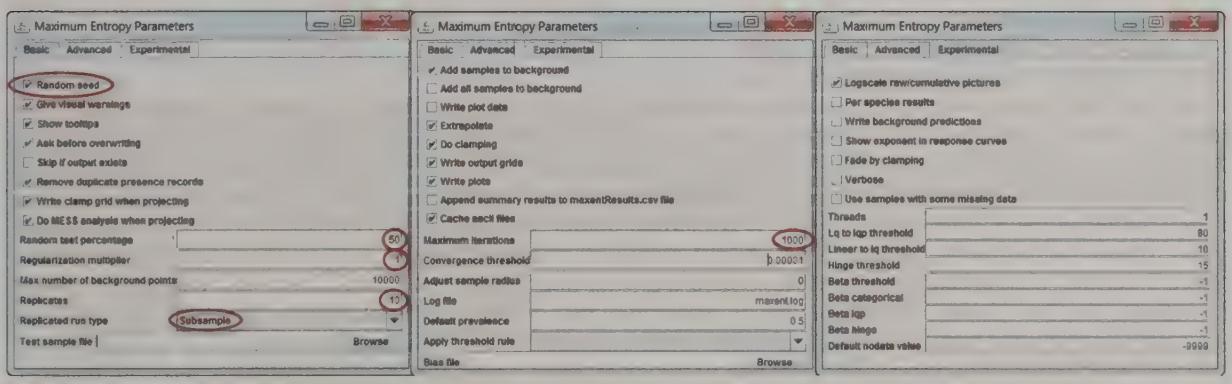

Figure 2.6. All of MaxEnt input parameters (except the six circled in red) were left at their default values during the modeling process.

It is also important to point out that one input parameter, called regularization, was particularly critical for developing reasonable MaxEnt models. Regularization affects how closely the predicted distribution is fit to the distribution of the presence records and associated environmental variables (Phillips, 2012). Larger regularization values (>1) fit more general models to the training data producing more global predictions, whereas small regularization values (<1) fit the predicted model closer to the training data producing more localized predictions. If the regularization value is too large or small, the prediction may be too general or too localized (respectively) and may not match well with the test data. Given this sensitivity, the regularization value (0.0001) applied by Tittensor et al. 2009 was used as a starting point. Three more regularization values above 0.0001 were tested (i.e., 0.01, 0.1 and 1) to determine the optimal value for this study. Highly variable response curves (produced from the models with regularization values = 0.0001, 0.01 and 0.1) suggested that these initial models were being overfit and that the regularization values were too small. When the regularization value was increased to one, the response curves smoothed out considerably and the overall performance of the model improved. Regularization values above one were not tested because the value of one performed well, and because larger values may have created models that were too general, which would have over-predicted the distribution of mesophotic corals.

2.6. MODEL EVALUATION

2.6.1. How was the performance and accuracy of MaxEnt models evaluated?

Two metrics were used to measure MaxEnt's performance and accuracy in predicting mesophotic hard coral presence in the Au'au Channel Region. These metrics specifically included: (1) receiver operating characteristic (ROC) curves, from which area under the curve (AUC) test statistics were calculated, and (2) an independent accuracy assessment of the genera models' commission errors and the general hard coral model's omission and commission errors. ROC curves (Figure 2.7) measure a model's predictive performance by comparing its sensitivity (i.e., true positive prediction rate) to its specificity (i.e., false positive prediction rate), as the habitat suitability threshold used to classify presence/absence varies. However, since MaxEnt does not use absence data, a randomly selected set of background points (i.e., a random sample of the full spectrum of environmental conditions in the study area without regard to presence/absence of corals) is used to estimate the models' specificity (Phillips et al. 2006). Together, specificity and sensitivity help describe the "rate" at which a MaxEnt model correctly versus incorrectly predicts the presence of mesophotic hard corals. This rate depends on the choice of a particular habitat suitability threshold value above which corals are classified as "present" and below which corals are classified as "absent." Instead of choosing one threshold to assess model performance, the threshold-independent test AUC statistic was used to measure the overall predictive performance of a model compared to a random guess. Test AUC values ranging from 0.7 to 0.8 denote "good" model performance; values from 0.8 to 0.9 denote "excellent" model performance, and values greater than 0.9 denote "outstanding" model performance (Hosmer and Lemeshow, 2000). Test AUC values at or below 0.5 indicate that the model's prediction was no better than one created by chance alone. It should be noted that, because MaxEnt uses background points rather than true absences to estimate specificity, the maximum possible test AUC value depends on what fraction of the study area is occupied by the species (maximum possible AUC = 1 - (a/2), where a = fraction of grid cells occupied by the species) (Wiley et al. 2003). When comparing models for widespread species to comparatively rarer species, one should keep in mind that the test AUC for more widespread species may be lower simply because of this upper bound on test AUC.

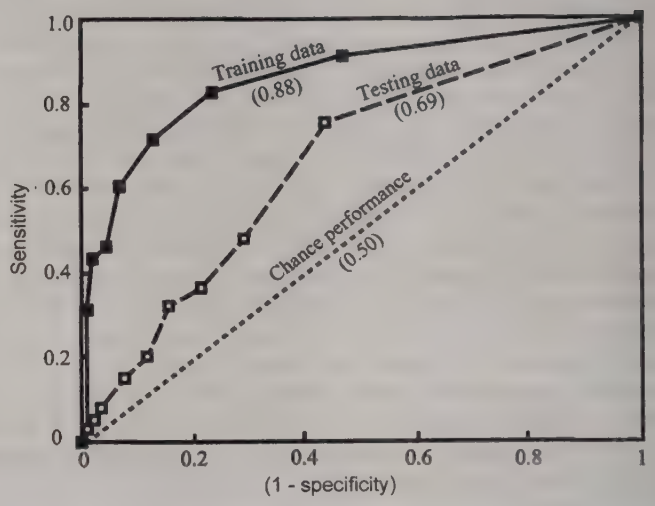

Figure 2.7. ROC curve showing how a model performs relative to chance. The numbers below each curve are example AUC values. Figure adapted from Fielding and Bell 1997.

In addition to ROC AUC values, an independent assessment of the models' omission and commission errors was conducted as another measure of MaxEnt's ability to generate reliable models. Omission errors describe the number of times that MaxEnt incorrectly predicted the absence of hard corals (sometimes referred to as a false negative). Commission errors denote the number of times that MaxEnt incorrectly predicted the presence of hard corals (sometimes referred to as a false positive). Together, these errors—along with the true positive (i.e., sensitivity) and true negative (specificity) values—describe the overall accuracy of the models' predictions. This accuracy assessment was conducted using a random 30% of the hard coral absence data (n = 4,332 points) and presence data (n = 852 points), neither of which were used during the model training process. Only absence data was used in this supplemental accuracy assessment of the genus-specific models because there were not enough presence records to set aside for model development.

Problems associated with the spatial autocorrelation of this assessment data were addressed by first analyzing the structure of the autocorrelation, and then selecting points for the accuracy assessment that were far enough apart to meet the assumption of statistical independence. Both global Moran's I and Anselin Local Moran's I statistics indicated the presence of significant spatial autocorrelation ($p \leq 0.0001$). Given this significance, a theoreti-

cal spherical variogram model was fit to an empirical variogram for the mesophotic hard coral data using nonlinear least squares. Parameters for the variogram model were the following: nugget = 0.5, partial sill = 0.04, and range = 107 meters. A spherical model was chosen because it qualitatively fit the empirical variogram the best, and because it is the only variogram model that includes a finite spatial range value (Kendall et al. 2005). The range of a variogram denotes the distance at which spatial autocorrelation becomes negligible. Given the range of the spherical model, assessment points separated by more than 107 m (n = 1,301 for absence and n = 345 for presence) were considered to be essentially independent and selected for this assessment (Figure 2.8). Confusion matrices were created using these spatially independent points for the general coral model at habitat suitability values in increments of 0.1. The proportion of correctly predicted presence and absence records was then graphed against these habitat suitability values to determine the tradeoff between the predictive accuracy and generalization of a model.

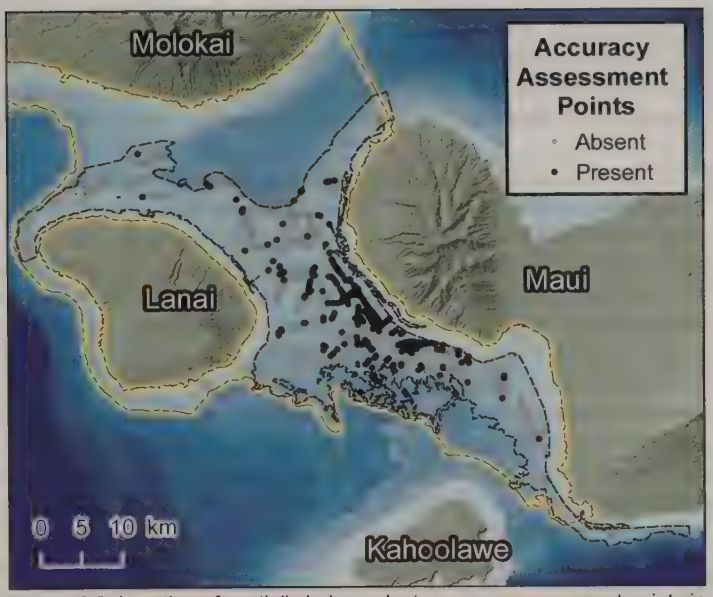

Figure 2.8. Location of spatially independent accuracy assessment points in Au'au Channel Region.

2.6.2. How were habitat suitability thresholds chosen?

The habitat suitability value (or threshold) chosen to denote coral presence affects the sensitivity, specificity and thus, overall accuracy of the prediction. If an extremely high suitability value is chosen to denote predicted presence (e.g. 0.8-1 for a very specific model), very little of the study area will be deemed suitable habitat. Accuracy (i.e., specificity) will be very high for sites correctly identified as lacking corals and low for sites correctly classified as having them. If a very low suitability value is chosen to denote predicted presence (e.g. 0.1 for a very sensitive model), a large proportion of the study area will be deemed suitable habitat. This has the effect of producing very high accuracy for sites confirmed as having hard corals (i.e., sensitivity) but low accuracy for sites lacking them.

Given the tradeoffs in sensitivity and specificity, the question arises of what suitability value should be applied for a given application. There are several approaches to selecting a threshold value, each with merits and drawbacks (Fielding and Bell 1997, Liu et al. 2005). For this study, we chose to focus on the suitability value where combined sensitivity and specificity reach the highest level. For suitability values in increments of 0.1, we added the proportion of correctly classified presences and absences to identify the suitability of maximum combined sensitivity (the probability that the model will correctly predict presence) and specificity (the probability that the model will correctly predict absence), hereafter noted as MCSS. Note that this MCSS number (derived from the independent accuracy assessment data) is based on a random subset of data and may vary slightly if a different subset were drawn.

MaxEnt provides a similar MCSS value based on the subset of presence data used to create the ROC curve. MaxEnt's MCSS value is created using a subset of actual presence data just like the supplemental accuracy assessment described above, however instead of actual absences as were used above, pseudo absences are used. Recall that pseudo-absences are simply randomly selected locations in the study area where coral presence data is lacking and corals are assumed to be absent. MaxEnt provided the MCSS value for each of the 10 model replicates that were run. We averaged these values across the 10 replicates for hard coral and each genus respectively. For each averaged model, we mapped grid cells above and below this suitability threshold as coral = present and coral = absent, respectively. We also show two hypothetical management situations (above and below this threshold) to further demonstrate the tradeoffs in model sensitivity and specificity. Specifically, we

mapped values where this MCSS suitability was decreased by 50% (to demonstrate a situation where sensitivity was half as important as specificity) and increased by 50% (situation where specificity was more important). Note that as with the MCSS value above (derived from independent accuracy assessment data), this MCSS number is based on random data subsets and may vary slightly if different subsets are drawn.

2.6.3. Which variable(s) mattered most to the models?

In addition to understanding the performance and accuracy of the MaxEnt models, two different metrics were used to quantify the contribution of each environmental variable to each predictive model and its performance. These metrics included: (1) permutation importance and (2) jackknife analysis. Permutation importance denotes the reduction in test AUC (expressed as %) of the final MaxEnt model when variables' values are randomly permutated. A large drop in permutation importance indicates that the model is heavily dependent on that particular variable, while a small drop indicates that the predictor does not contribute much new information (i.e. the information it contains is redundant) (Phillips 2012). Jackknife analysis measures the contribution of each variable to a model's gain (goodness of fit), and its impact on test AUC values. It does so by creating both (1) MaxEnt models using only one variable at a time, and (2) MaxEnt models that exclude one variable at a time. This process of inclusion and exclusion isolates the contribution of each predictor variable from the other variables, and describes whether a particular variable improves or degrades the performance of a model. These two metrics were analyzed together and compared with each other to determine which variable(s) were the most influential and reliable predictors. Variables with permutation values > ~10% and single variable jackknife test AUC values > ~0.75 were considered important predictors of mesophotic coral presence in the Au'au Channel Region. Response curves were used to describe how habitat suitability changed logistically with the values of these predictors either in the context of a hypothetical single-variable model (single variable response curves) or in the context of the full multi-variable model with all other predictors held at their averages (multi-variable response curves). It should be noted that the multi-variable response curves were the actual models used to generate the final MaxEnt predictions, while single-variable response curves were simply produced to help with model interpretation.

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Four separate MaxEnt models were created for predicting: 1) all mesophotic hard corals combined, 2) *Leptoseris*, 3) *Montipora*, and 4) *Porites*. For each model, we report overall fit and performance, a map of predicted environmental suitability, prevalence of mesophotic corals in field data and model results, environmental variables of importance to the prediction based on permutation and jackknife tests, and response curves showing how the range of values for each of the important environmental variables affects the probability of suitable mesophotic coral habitat. Following the results for individual genera, models are compared on the basis of the predicted distributions, list of influential variables, and differences in habitat partitioning.

3.1. ALL MESOPHOTIC CORALS

Mesophotic corals were observed in 16% of the ROV records in the study area (Table 2.1). The average test AUC (0.900) for the model of predicted distribution of all mesophotic corals combined indicated 'excellent' overall model performance (defined in Hosmer and Lemeshow 2000; maximum AUC = 1-[0.16/2] = 0.92). The supplemental accuracy assessment based on a randomly selected 30% of absence and presence records revealed the tradeoff between habitat suitability values and the proportion of accuracy assessment points correctly classified as present or absent (Figure 3.1). The point where the sum of these two types of prediction accuracy (i.e., correct presence and correct absence) is maximized, or the MCSS, occurred at a moderate suitability value of 0.3. This balances the two types of errors and correctly predicts both coral presence and absence at over ~73.1% of sites (Table 3.1). Note that these performance and accuracy statistics are based on a random subset of data and results will vary slightly if different subsets were drawn.

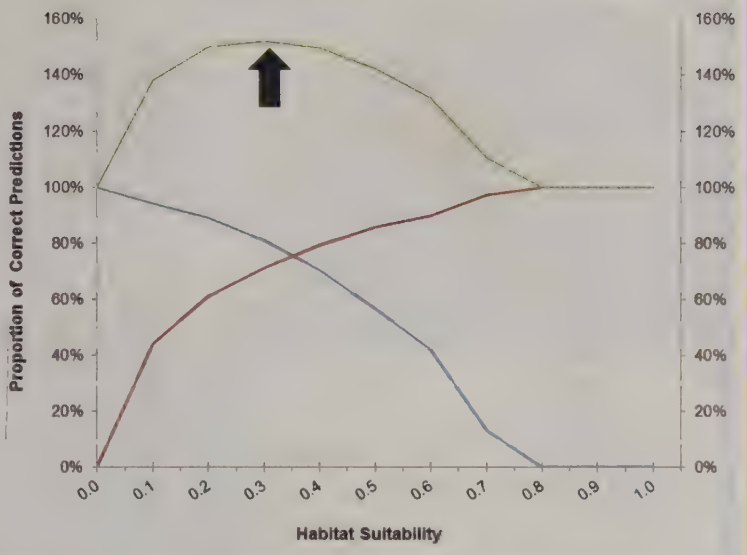

Figure 3.1. Proportion of accuracy assessment sites correctly predicted as having hard corals present (blue) and absent (red) as a function of MaxEnt habitat suitability value chosen to denote coral presence. Correct presence and absence values are added and shown (green) with an arrow indicating the maximum sum.

Predicted probability of suitable environmental conditions for mesophotic corals overall were highest in a broad region in the eastern half of the Au'au Channel in the area of the Lahaina Roads Basin and Lahaina Pinnacles

Table 3.1. Two methods were used to describe predictive performance and accuracy of the MaxEnt models. The first method (a) withheld randomly selected data from the training dataset to assess each model run's performance. The second method (b) randomly selected a data subset, which was not used during the training process, to independently assess the predictive accuracy of these ensemble models.

MODEL	(A) CROSS VALIDATION*			(B) INDEPENDENT ACCURACY ASSESSMENT*			
	MEAN MAXENT THRESHOLD (± 1 σ)	MEAN TEST AUC (± 1 σ)	MAXIMUM TEST AUC	MAXENT THRESHOLD	PRESENCE PRODUCER'S ACCURACY (%)	ABSENCE PRODUCER'S ACCURACY (%)	OVERALL ACCURACY (%)
All Hard Corals	0.25 ±0.029	0.90 ±0.002	0.92	0.30	80.9	71.0	73.1
Montipora	0.15 ±0.025	0.97 ±0.003	0.98	0.15	-	86.1	-
Porites	0.07 ±0.040	0.95 ±0.027	0.95	0.07	-	85.3	-
Leptoseris	0.20 ±0.022	0.93 ±0.006	0.98	0.20	-	78.2	-

* These numbers are based on random subsets, and may changed based on the subset drawn.

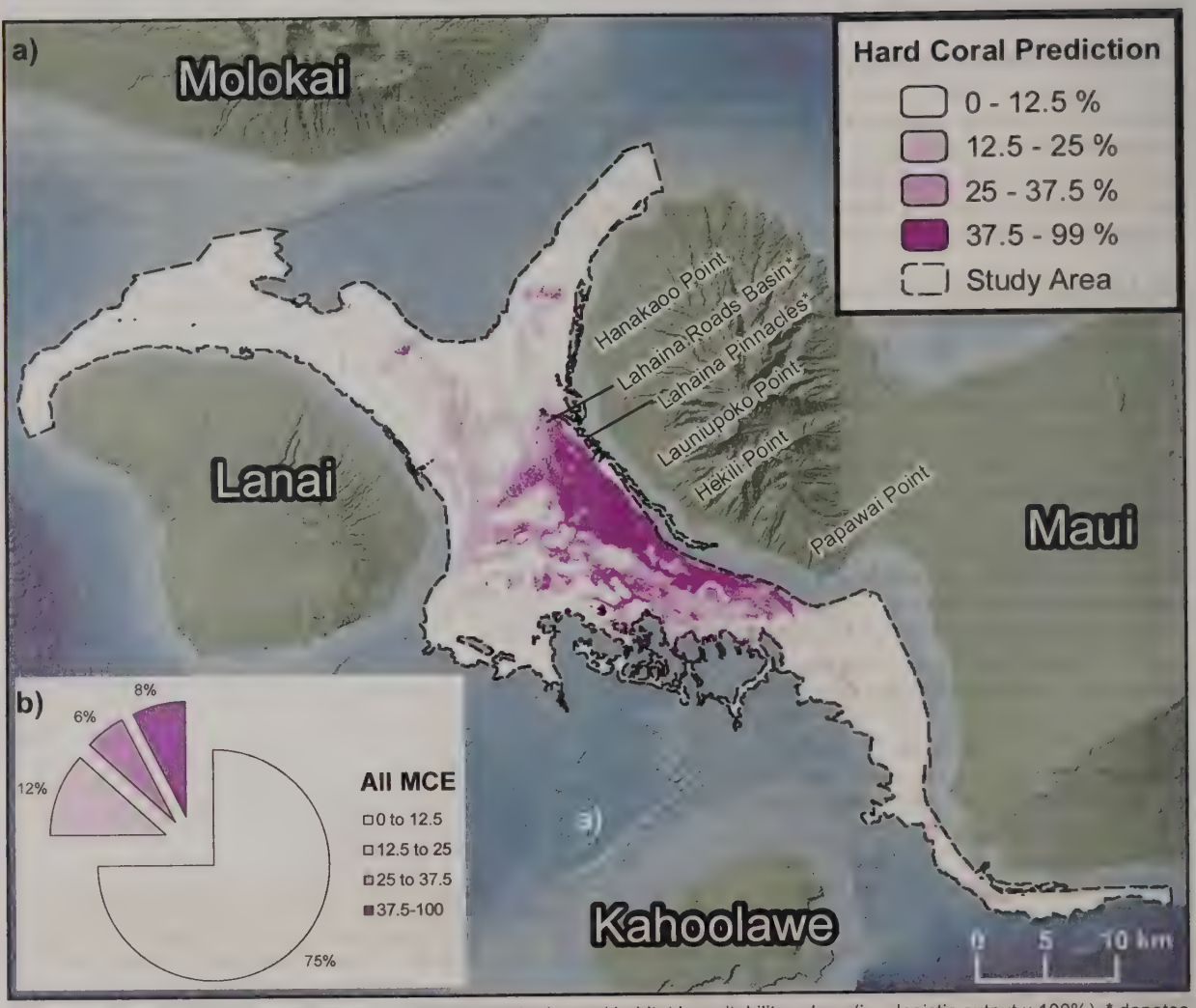

Figure 3.2a and b. a) Predicted distribution of hard mesophotic coral habitat by suitability values (i.e., logistic output x 100%). * denotes feature described in Grigg et al. 2002. b) Proportion of the study area by suitability values for all hard corals.

between Hanakaoo Point and Papawai Point (Figure 3.2a). Highly suitable conditions were also seen along the drowned ridges at the edge of the study depths south of Hekili Point. There were also disconnected pockets of more moderate suitability in other parts of the study area. Using the ROC curves, combined sensitivity and specificity was maximized at a mean suitability value of 0.25 ±0.03 (±SD, n =10,Table 3.1). (Table 3.1). Eighty seven percent of the study area had suitability values below this maximized value (Figure 3.2b). Only 8% of the study area had suitability value above 0.375, the highest threshold that we considered. Seventy five percent of the study area has suitability values below 0.125, the lowest that we considered. Note that these numbers are also based on a random subset of data and results will vary slightly if a different subset were drawn.

Key environmental variables for predicting mesophotic corals overall were partly identified through the permutation test wherein each variable was evaluated for its contribution to the MaxEnt model by randomly shuffling its values and measuring the reduction in AUC expressed as a percentage (Table 3.2). Based on permutation importance, influential variables were mean euphotic depth (28.9% reduction in AUC when randomized), mean depth calculated at the 200 m analysis scale (16.7% reduction in AUC), and standard deviation of euphotic depth (15.3% reduction in AUC). The jackknife test revealed that when used alone as predictors, a similar list of variables emerged as having relatively high AUC values including mean and standard deviation of euphotic depth (AUC = 0.78 and 0.79) and mean depth at any scale (AUC = 0.73 to 0.74) (Figure 3.3). Additions to these were mean sea surface temperature with an AUC of 0.82 and also distance to shore at any scale with an AUC of 0.72

Table 3.2. Important variables for each model as measured by permutation. For each environmental variable in turn, the values of that variable on training presence and background data are randomly permuted. The model is re-evaluated on the permuted data and the drop in AUC compared to the model based on the actual data is shown as a percentage. Permutation importance values ≥ 5 are in bold font.

	PERMUTATION IMPORTANCE			
VARIABLE	**ALL HARD CORALS**	***LEPTOSERIS***	***MONTIPORA***	***PORITES***
aspect_010m	0.2	0.5	0.2	0.2
aspect_025m	0.3	0.6	0.2	1.1
aspect_200m	2.6	5	1.3	0.1
bathymetry_010m	**5.6**	**7**	**17.9**	**12.5**
bathymetry_025m	2.6	**9.9**	2.5	**38.3**
bathymetry_200m	**16.7**	**6.7**	**6.9**	0.4
bpibroadstnd_010m	0.2	0.5	0.9	0.2
bpibroadstnd_025m	0.4	0.9	0.8	0.1
bpibroadstnd_200m	0.1	0	**5.4**	0
currentsmean35m_010m	1.6	1.3	0.3	2.8
currentsmean85m_010m	1.4	1.4	2.6	0.9
currentsvar35m_010m	0.4	**6.9**	3.8	0
curvature_010m	0.1	0.1	0.1	0
curvature_025m	0.2	0.2	0.6	0
curvature_200m	0.4	0.2	2.7	0.1
curvatureplan_010m	0	0.1	0.1	3.5
curvatureplan_025m	0.2	0.2	1.1	0.2
curvatureplan_200m	0.6	1	0.4	1.7
curvatureprofile_010m	0.1	0.1	0.1	0.2
curvatureprofile_025m	0.3	0.3	0.3	3.4
curvatureprofile_200m	0.7	0.5	0.9	0.1
distancetoshore_010m	**5.3**	3.1	**5.1**	0
distancetoshore_025m	0.4	0.7	0.6	0
distancetoshore_200m	3.9	1.2	2.5	**7.5**
euphoticdepthmean_010m	**28.9**	**16.6**	**25.3**	**13**
euphoticdepthstdev_010m	**15.3**	**9.7**	2.6	**8.5**
rugosity_010m	0.2	0.3	0.2	0.3
rugosity_025m	0.5	0.6	0.1	0.2
rugosity_200m	0.6	2.4	1.9	0.4
slopeofslope_010m	0.3	0.4	0.5	0.1
slopeofslope_025m	0.4	1	0.3	0.3
slopeofslope_200m	**5.7**	**11.8**	0.5	0.1
sstmean_010m	3.1	1.9	**10.7**	2.7
sststdev_010m	0.6	**6.9**	0.9	1

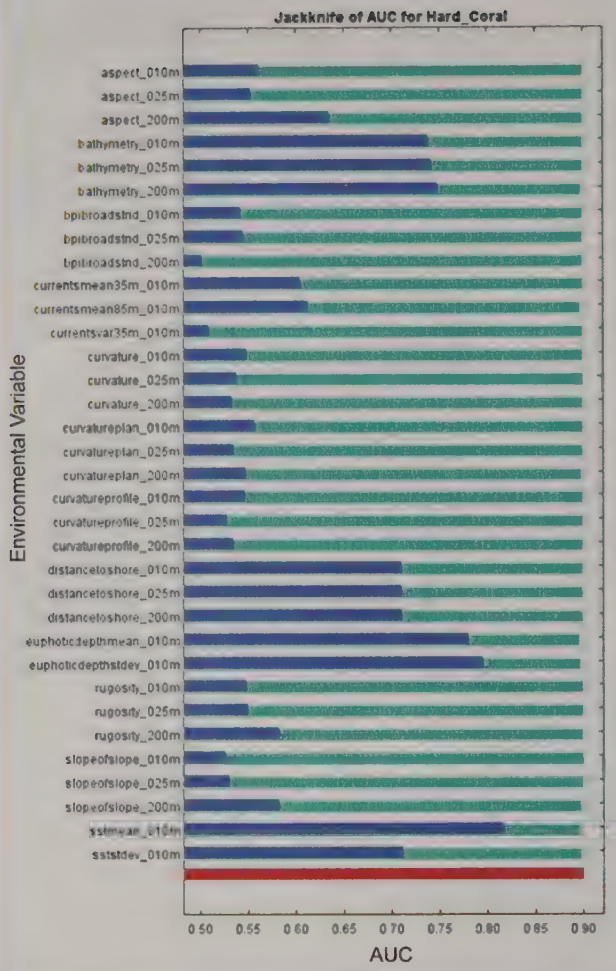

Figure 3.3. Important variables in the all hard coral model as measured by jackknife of AUC. AUC is shown for the model with all variables (red), and for models without each variable (teal), and models based on only each individual variable (blue).

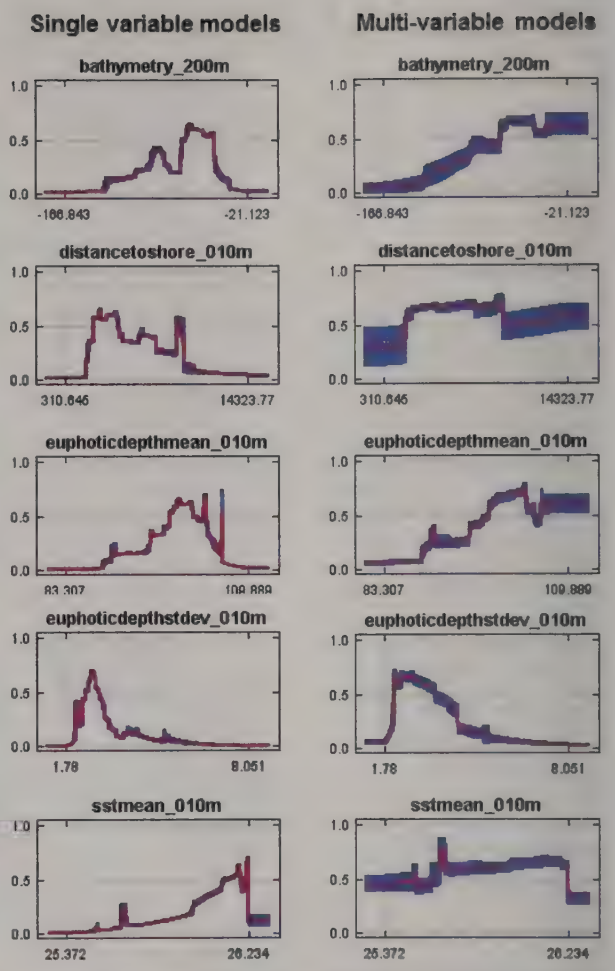

Figure 3.4. Response curves for environmental variables important to the all hard coral habitat prediction. Single variable models exclude all other variables from the logistic prediction. Multi-variable models hold all other variables at their average values in the logistic prediction.

when used as the sole predictor. Also of note, the elimination of single variables from the modeling process did not result in a large decline in AUC compared to the whole model. This indicates that the model is not dependent on any single variable and suggests that a high degree of redundant information is included in the model via correlated predictor variables.

Response curves show how each environmental variable affects the MaxEnt prediction for mesophotic corals in logistic format. Only those variables noted as important in the permutation or jackknife tests are addressed here. The full suite of response curves for all variables is shown in Appendix A (contact lead author). When all other variables are held at their average values, mean depth appears to have an influence of decreasing environmental suitability as depth increases with lowest suitability deeper than ~115 m (Figure 3.4). When only depth is used as a predictor, the response pattern is similar except that the very shallowest areas are deemed unsuitable (Figure 3.4) and there is a clear peak in suitability between 45 and 75 m depth. When all other variables were held to their average values, euphotic depth showed a pattern of increasing suitability with higher values until leveling off or declining at around 100 m. When used alone, euphotic depth showed a pattern of peak suitability around 100 m with additional spikes in suitability at higher values. When all other variables were held to their average values, standard deviation of euphotic depth showed a sudden increase in suitability at around 2 and then steadily declined as variance increased reaching unsuitable conditions at values of 5 and higher. When used alone, standard deviation of euphotic depth showed a similar but more variable pattern. When all other variables

are held to their average values, distance to shore showed highest suitability between 2 and 9 km. When used alone, three clear peaks in suitability were observed. These were centered at 3.5, 6.5 and 9 km from shore. Last, when all other variables were held to their average values or when used alone, suitability increased with sea surface temperature and showed a spike in suitability at 25.65°C.

3.2. *MONTIPORA*

Montipora was observed in 3.5% of the field observations (Table 2.1). The average test AUC (0.967) for the model of predicted distribution of *Montipora* indicated 'outstanding' overall model performance (Hosmer and Lemeshow 2000; maximum AUC = 1-[0.04/2] =0.98). Four concentrations of field observations were evident including the middle of the Au'au Channel off Lahaina, the Lahaina Pinnacles area, ~4.5 km off Launiupoko Point, and ~3.5 km off Hekili Point. The supplemental accuracy assessment indicated that the model correctly predicted coral absence at 86.1% of sites (based on MCSS suitability of <0.15 denoting absence). Predicted probability of suitable environmental conditions for *Montipora* was highest in the region of the Lahaina Pinnacles and 3.5 km south and southeast of Hekili Point (Figure 3.5a). Using the ROC curves, combined sensitivity and specificity was maximized at a suitability value of 0.15 ±0.03 or 1σ (Table 3.1). Ninety six percent of the study area had suitability values below this maximized value (Figure 3.5b). Only 3% of the study area had suitability value above 0.225, the highest threshold that we considered. Ninety two percent of the study area has suitability values below 0.075, the lowest that we considered.

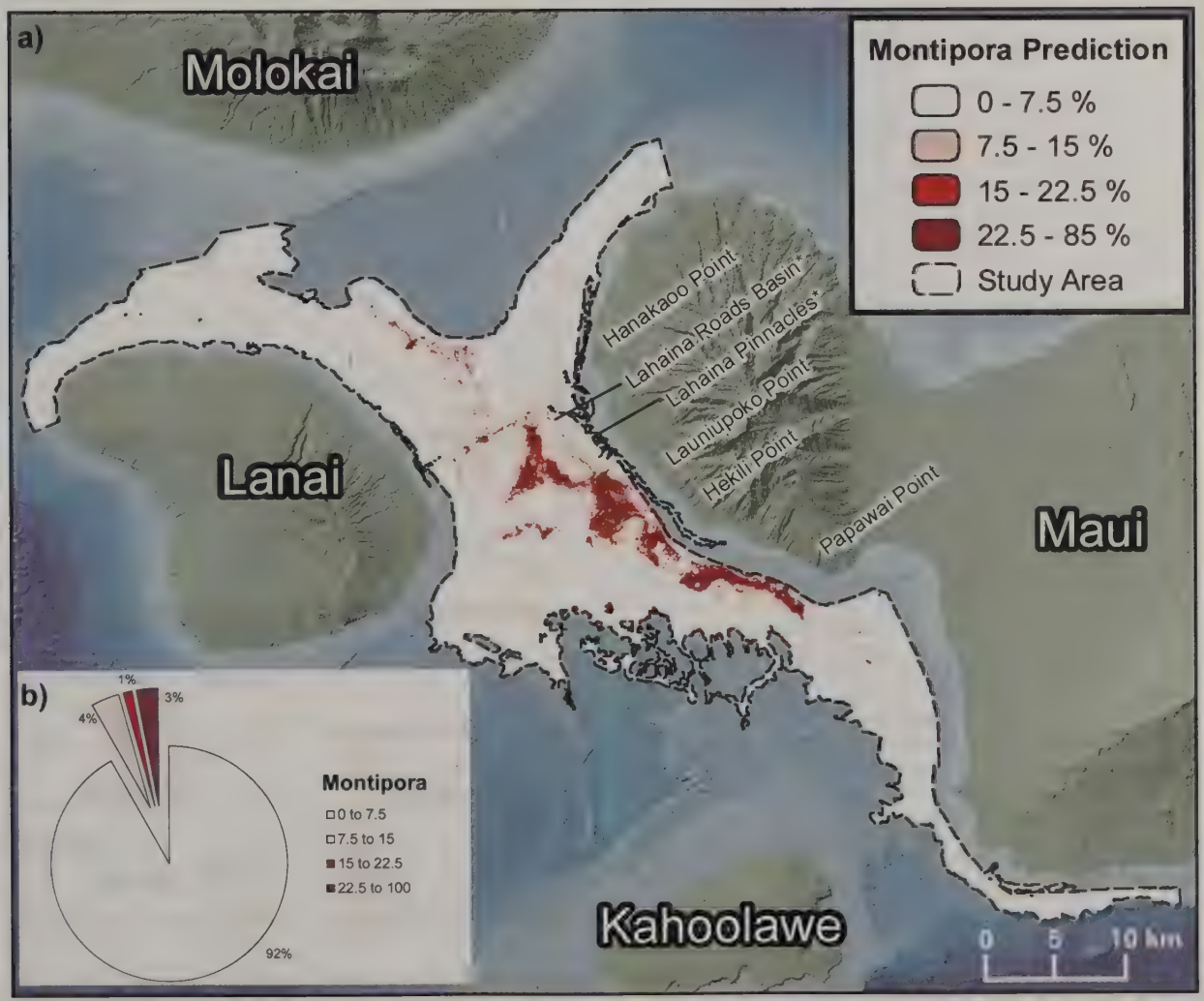

Figure 3.5a and b. a) Predicted distribution of *Montipora* habitat by suitability values (i.e., logistic output x 100%). * denotes feature described in Grigg et al. 2002. b) Proportion of the study area by suitability value for *Montipora*.

Key environmental variables for predicting *Montipora* identified through the permutation test (Table 3.2) were mean euphotic depth (25.3% reduction in AUC when its values were randomized), mean depth calculated at the 10 m analysis scale (17.9% reduction in AUC), and mean sea surface temperature (10.7% reduction in AUC). The jackknife test revealed that when used alone, a similar list of variables emerged as having relatively high AUC values including mean and standard deviation of euphotic depth (AUC = 0.92 and 0.85), sea surface temperature (AUC = 0.87), and mean depth at any scale (AUC = 0.81) (Figure 3.6). Additions to this group were distance to shore measured at any scale (AUC = 0.77). Also of note, the elimination of single variables from the modeling process did not result in a large decline in AUC compared to the whole model. This indicates that the model is not dependent upon any single variable and the influence of individual variables can be mostly explained or accounted for by correlated variables as well.

Response curves show how each environmental variable affected the MaxEnt prediction for *Montipora* in logistic format. Only those variables noted as important in the permutation or jackknife tests will be addressed here with the full suite of response curves for all variables shown in Appendix A (contact lead author). When all other variables were held to their average values, euphotic depth showed a pattern of peak suitability at depths between 99 and 104 m with two much smaller peaks at 90 and 96 m (Figure 3.7). When used alone, euphotic depth showed 4 clear peaks in suitability at 91, 96, 99 and 104 m. When all other variables were held to their average values, standard deviation of euphotic depth showed a plateau of high suitability between 2.5 and 4.3. When used alone, standard deviation of euphotic depth showed a tight cluster of four peaks at values between 2.5 and 3.9. When all other variables were held to

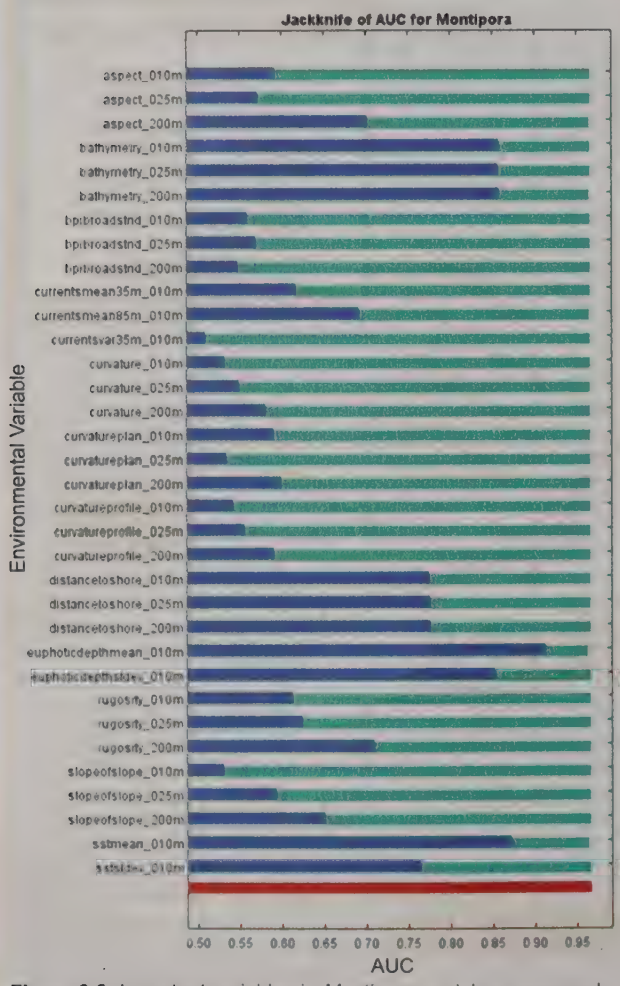

Figure 3.6. Important variables in *Montipora* model as measured by jackknife of AUC. AUC is shown for the model with all variables (red), and for models without each variable (teal), and models based on only each individual variable (blue).

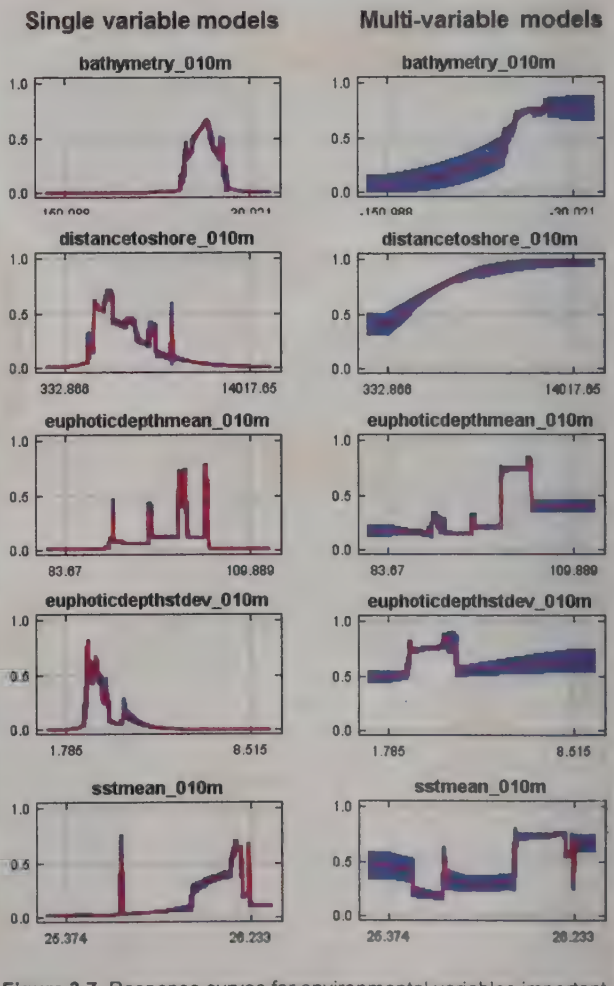

Figure 3.7. Response curves for environmental variables important to *Montipora* prediction. Single variable models exclude all other variables from the logistic prediction. Multi-variable models hold all other variables at their average values in the logistic prediction.

their average values, depth calculated at the 10 m scale shows a pattern of low suitability in deep regions with rapidly increasing suitability beginning at 75 m into shallower areas (Figure 3.7). When used alone, depth measured at the 10 m scale showed peak suitability between 45 and 75 m depth. When all other variables were held to their average values, distance to shore showed increasing suitability with higher values. When used alone, distance to shore measured at any scale also showed four or more distinct peaks of suitability. These were at 3.5, 5, 7, and 8.1 km from shore. Last, when all other variables were held to their average values, suitability for mean sea surface temperature showed a spike at 25.65°C and a plateau of high suitability between 25.95 and 26.2 °C. When used alone, suitability showed three distinct peaks at values 25.64, 26.15, and 26.22 °C.

3.3. *PORITES*

Porites was observed in <1% of the field observations (Table 2.1). The average test AUC (0.952) for the model of predicted distribution of *Porites* indicated 'outstanding' overall model performance (Hosmer and Lemeshow 2000; maximum AUC=1-[0.1/2]=0.95). The supplemental accuracy assessment indicated that the model correctly predicted coral absence at 85.3% of sites (based on MCSS suitability of <0.07 denoting absence). Predicted probability of suitable environmental conditions for *Porites* was highest in a focused region along the eastern side of the Au'au Channel between Hanakaoo Point and Hekili Point with a hotspot in the vicinity of the Lahaina Pinnacles (Figure 3.8a). Using the ROC curves, combined sensitivity and specificity was maximized at a mean suitability value of 0.07 ±0.04 (±SD, n =10,Table 3.1). Ninety two percent of the study area had suitability values below this maximized value (Figure 3.8b). Only 5% of

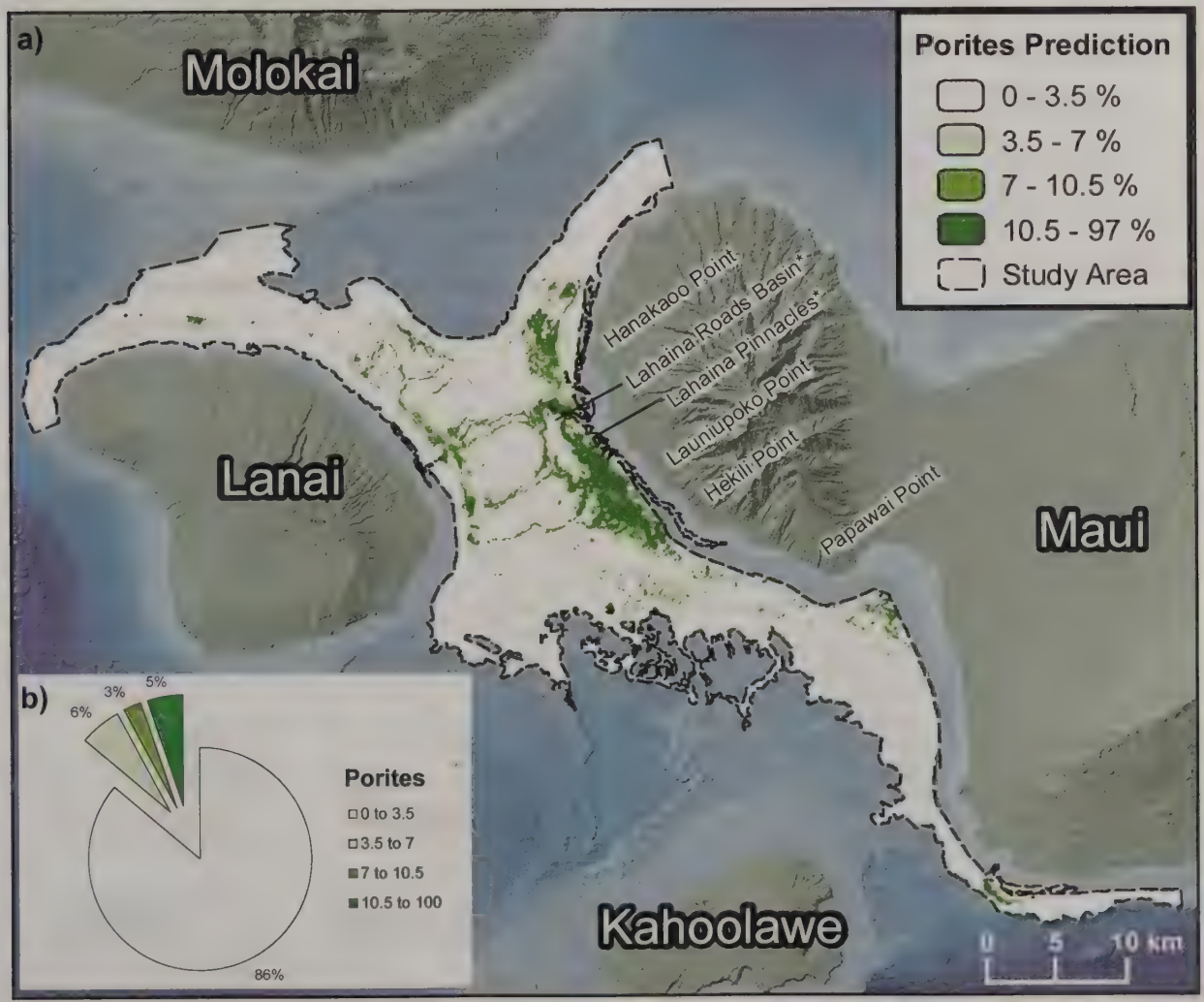

Figure 3.8a and b. a) Predicted distribution of *Porites* habitat by suitability values (i.e., logistic output x 100%). * denotes feature described in Grigg et al. 2002. b) Proportion of the study area by suitability value for *Porites*.

the study area had suitability value above 0.105, the highest threshold that we considered. Eighty six percent of the study area has suitability values below 0.035, the lowest that we considered.

Key environmental variables for predicting *Porites* identified through the permutation test (Table 3.2) were mean depth calculated at the 10 and 25 m analysis scales (12.5% and 38.3% reductions in AUC when their values were randomized respectively). The jackknife test revealed that when used alone, bathymetry again emerged as having relatively high AUC values (AUC = 0.85 to 0.86) (Figure 3.9). Additional variables of importance using the jackknife approach were distance to shore at any scale (AUC = 0.79), and mean euphotic depth and its standard deviation (AUC = 0.82 and 0.84). Also of note, the elimination of single variables from the modeling process did not result in a large decline in AUC compared to the whole model. This indicates that the *Porites* model is not dependent upon any single variable and the influence of individual variables can be mostly explained or accounted for by correlated variables as well.

Response curves show how each environmental variable affected the MaxEnt prediction for *Porites* in logistic format. These single variable response curves were smoother than the response curves for all hard corals, *Montipora* and *Leptoseris* because they were built with the fewest number of records. Only those variables noted as important in the permutation or jackknife tests will be addressed here with the full suite of response curves for all variables shown in Appendix A (contact lead author). When all other variables were held to their average values, mean depth calculated at the 10 or 25 m scales showed a pattern of increasing suitability with shallower waters (Figure 3.10). When used alone, mean depth calculated at the 10 or 25 m scales showed a distinct peak in suitability at 45-50 m. When all other variables were held to their average values, distance to shore showed little variation in suitability across values at the 10 and 25 m analysis scales. At the 200 m analysis scale, a sudden increase in suitability was observed at 2.5 km from shore followed by a gradual decline in suitability with higher values. When used alone, distance to shore measured at any scale showed a distinct peak of

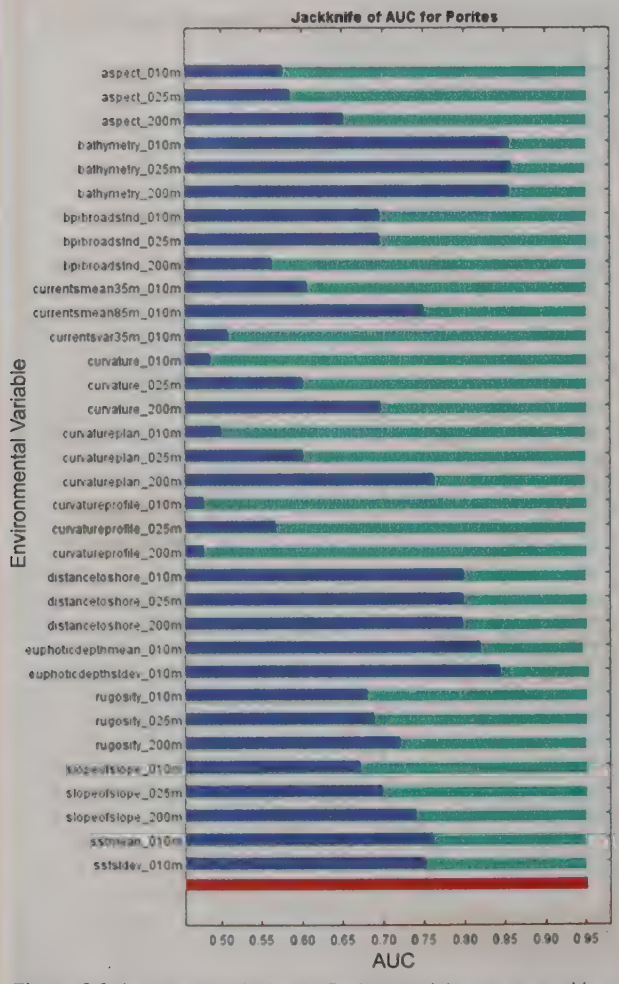

Figure 3.9. Important variables in *Porites* model as measured by jackknife of AUC. AUC is shown for the model with all variables (red), and for models without each variable (teal), and models based on only each individual variable (blue).

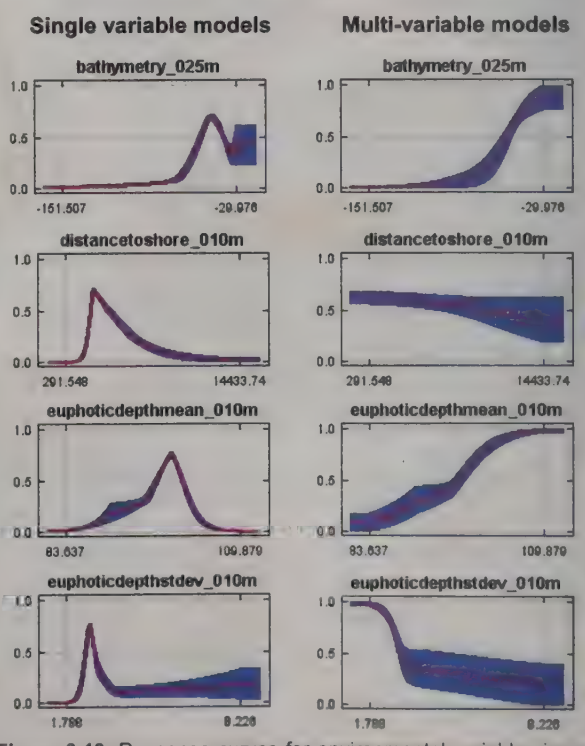

Figure 3.10. Response curves for environmental variables important to *Porites* prediction. Single variable models exclude all other variables from the logistic prediction. Multi-variable models hold all other variables at their average values in the logistic prediction.

suitability at 2.5 km from shore followed by a rapid decline in suitability. Of note, there were few field surveys conducted closer to shore than this distance. When all other variables were held to their average values, mean euphotic depth showed a gradual increase to very high suitability with deeper values. When used alone, mean euphotic depth showed a distinct peak at 99 m. When all other variables were held to their average values, standard deviation of euphotic depth showed high suitability at low values and then a rapid decline in suitability as variance increased. When used alone, standard deviation of euphotic depth showed a distinct peak at 2.7.

3.4. *LEPTOSERIS*

Leptoseris was observed in 3.6% of the field observations (Table 2.1). The test AUC (0.930) for the model of predicted distribution of *Leptoseris* indicated 'outstanding' overall model performance (Hosmer and Lemeshow 2000; maximum AUC = 1-[0.04/2] =0.98). The supplemental accuracy assessment indicated that the model correctly predicted coral absence at 78.2% of sites (based on MCSS suitability of <0.2 denoting absence). Predicted probability of suitable environmental conditions for *Leptoseris* was highest in the south/central region of the Au'au Channel off of Hekili Point (Figure 3.11a). Highly suitable conditions were predicted along many edges of drowned basins and ridge tops with a hotspot of suitability located at 20°46' N, 156°41' S. Using the ROC curves, combined sensitivity and specificity was maximized at a mean suitability value of 0.20 ±0.02 (±SD, n =10, Table 3.1). Ninety one percent of the study area had suitability values below this maximized value (Figure 3.11b). Only 5% of the study area had suitability

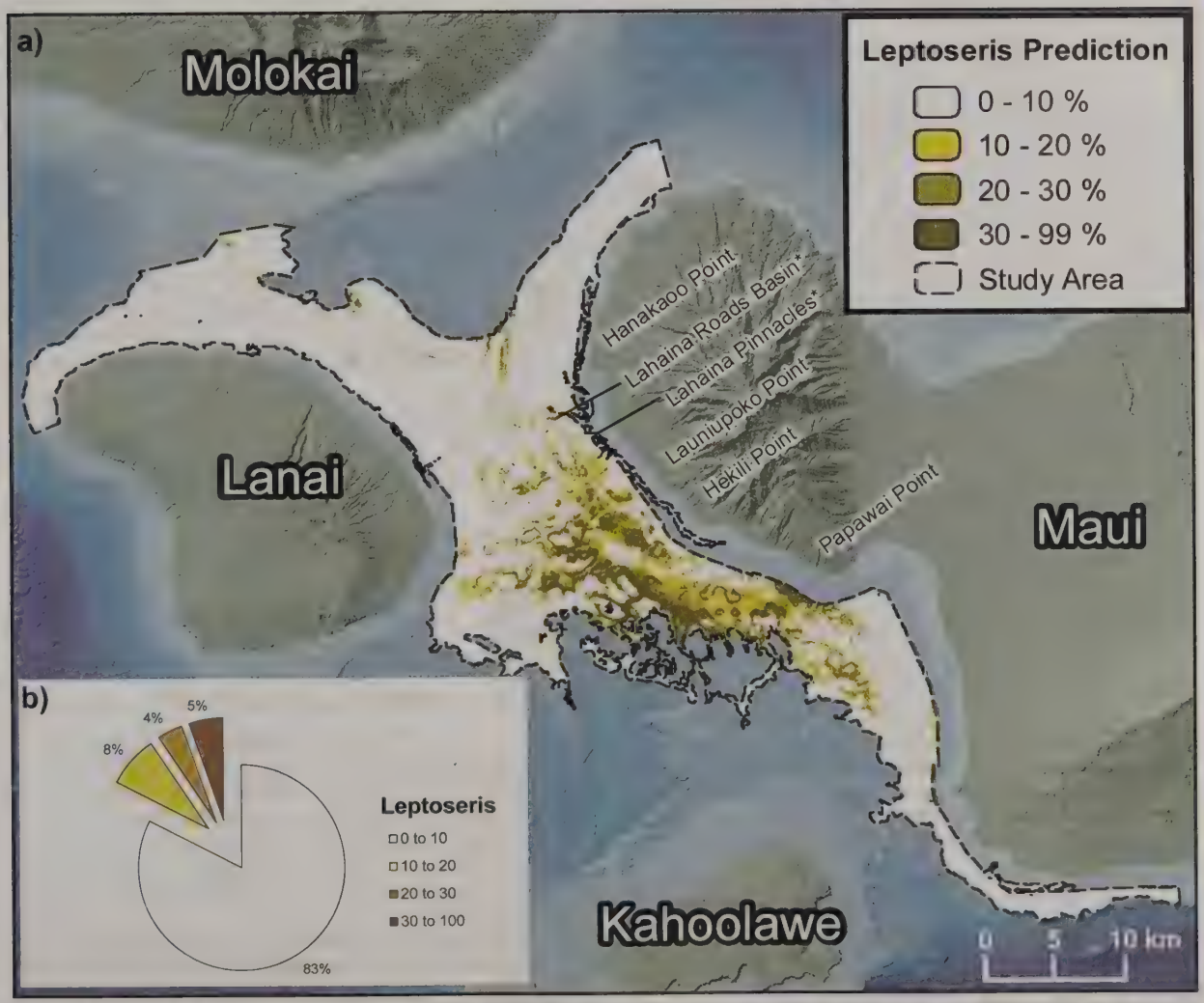

Figure 3.11a and b. a) Predicted distribution of *Leptoseris* habitat by suitability values (i.e., logistic output x 100%). * denotes feature described in Grigg et al. 2002. b) Proportion of the study area by suitability value for *Leptoseris*.

value above 0.3, the highest threshold that we considered. Eighty three percent of the study area has suitability values below 0.1, the lowest that we considered.

More variables were deemed important for *Leptoseris* than for other models. Key environmental variables for predicting *Leptoseris* identified through the permutation test (Table 3.2) were slope of the slope measured at the 200 m analysis scale (11.8% reduction in AUC when its values were randomized), mean euphotic depth and its standard deviation (16.6% and 9.7% reduction in AUC respectively), and mean depth calculated at the 25 m analysis scale (9.9% reduction in AUC). The jackknife test revealed that when variables were used alone, a similar list emerged as important by having relatively high AUC values. These were mean and standard deviation of euphotic depth (AUC = 0.79 and 0.76), mean depth at any scale (AUC = 0.77 to 0.78), and slope of the slope at the 200 m analysis scale (AUC = 0.77) (Figure 3.12). Additions to this group were distance to shore at any scale (AUC = 0.78), rugosity measured at the 200 m scale (AUC = 0.76), and mean sea surface temperature and its standard deviation (AUC = 0.81 and 0.78). Also of note, the elimination of single variables from the modeling process did not result in a large decline in AUC compared to the whole model. This indicates that the *Leptoseris* model is not dependent on any single variable and the influence of individual variables can be mostly explained or accounted for by closely correlated variables as well.

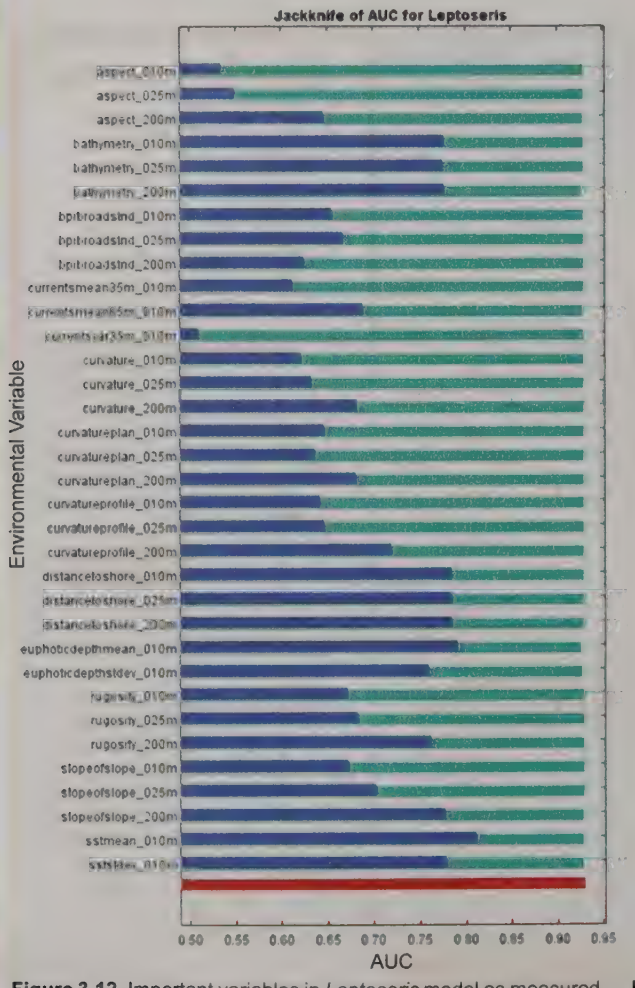

Figure 3.12. Important variables in *Leptoseris* model as measured by jackknife of AUC. AUC is shown for the model with all variables (red), for separate models formulated without each variable (teal), and for separate models formulated with only each individual variable (blue).

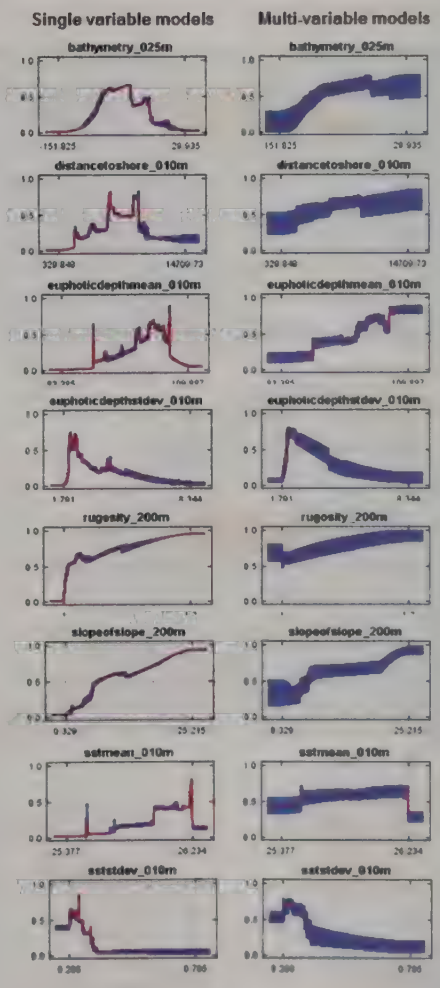

Figure 3.13. Response curves for environmental variables important to *Leptoseris* prediction. Single variable curves are based on single-variable MaxEnt models that excluded all other variables. Multi-variable response curves are based on varying the value of the indicated predictor in the final full MaxEnt model while holding all other variables at their average values.

Response curves show how each environmental variable affected the MaxEnt prediction for *Leptoseris* in logistic format. Only those variables noted as important in the permutation or jackknife tests will be addressed here with the full suite of response curves for all variables shown in Appendix A (contact lead author). When all other variables were held at their average values or when used by itself, slope of the slope appears to have an influence of increasing environmental suitability as values increase (Figure 3.13). When all other variables were held to their average values, depth at the 200 m scale shows a peak in suitability around 70 m depth (Figure 3.13). Depth measured at the 10 and 25 m scales showed generally high suitability values from shallow regions to depth of 110 m before declining. When used alone, depth measured at all scales showed a clear peak in suitability between 80 and 110 m depth and a smaller peak at 65 m. When all other variables were held to their average values, euphotic depth showed a pattern of increasing suitability with deeper values. When used alone, euphotic depth showed a pattern of peak suitability between 98 and 106 m with occasional spikes in suitability at lower values. When all other variables were held to their average values, standard deviation of euphotic depth showed a sudden increase in suitability at around 2 and then steadily declined as variance increased reaching unsuitable conditions at values of 5 and higher. When used alone, standard deviation of euphotic depth showed a similar but more variable pattern. When all other variables were held to their average values, distance to shore showed slightly increasing suitability at larger distances when measured at finer scales. When used alone, distance to shore measured at any scale showed highest suitability at moderate values with two high peaks in suitability at 6 and 9 km from shore and two smaller peaks at 2 and 4 km. When all other variables were held to their average values, rugosity measured at the 200 m scale showed a pattern of increasing suitability with higher values, reaching ~90% habitat suitability at highest rugosities. When used alone, rugosity measured at 200 m showed an exponential increase in predicted suitability before leveling off at very high suitability for higher rugosity. Last, when all other variables were held to their average values, suitability was flat for mean sea surface temperature, but when used alone, suitability gradually increased with warmer values and showed spikes in suitability at 25.5 and 26.2°C. Standard deviation of sea surface temperature showed higher suitability at low values whether used alone or when all other variables were fixed to their average values.

Image 2. The Pisces V submersible working on a mesophotic reef of *Leptoseris hawaiiensis* corals on a small rock outcrop at a depth of 102 m. Photo Credit: HURL.

Image 3. Scientist Ray Boland surveys fish communities on a low relief "carpet" of branching *Montipora capitata* corals. These reefs cover 10s of square kilometers of seafloor off the coast of West Maui. Photo Credit: J. Rooney.

3.5. COMPARISONS AMONG GENERA

The three genera, *Leptoseris*, *Montipora*, and *Porites* shared several variables deemed influential to each of their specific models. Important variables in models of all three genera included depth, distance from shore, mean euphotic depth, and variance of euphotic depth. Comparisons across the genera among the single variable response curves for these predictors offer some insight into how these three genera may partition the space in the Au'au channel region. Depth of peak suitability was shallowest for *Porites* (~43 m), deeper for *Montipora* (~59 m), and covered a broad but deeper still range of depths for *Leptoseris* (~82 m) (Figure 3.14a). Peak suitability for distance to shore was shortest for *Porites* (~2.4 km), slightly farther offshore for *Montipora* (~3.7 km), and farthest offshore for *Leptoseris* (peaks at ~6.1 and ~9 km) (Figure 3.14b). In contrast, to depth and distance to shore, mean and variance of euphotic depth showed broadly overlapping suitability for all 3 genera. *Leptoseris* had the deepest peak at euphotic depth of 106 m, followed by *Montipora* at 103 m and *Porites* at 99 m (Figure 3.14c). *Leptoseris* showed peak suitability in areas of lower variability in euphotic depth than *Porites* and *Montipora* (Figure 3.14d).

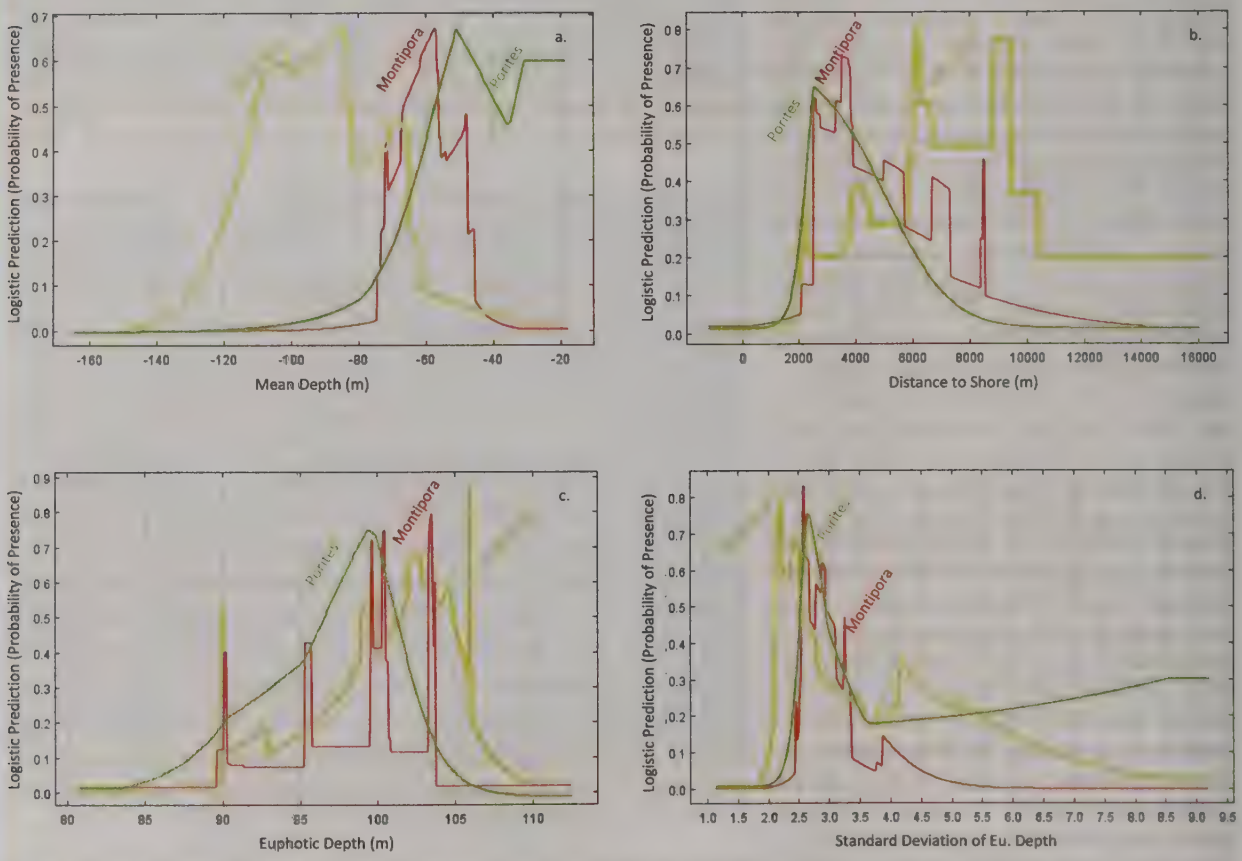

Figure 3.14a-d. Overlay of the *Leptoseris*, *Montipora*, and *Porites* single-variable MaxEnt response curves for the variables: (a) mean depth, (b) distance from shore, (c) mean euphotic depth, (d) and standard deviation of euphotic depth.

Comparing model results can be misleading when based on organisms with markedly differing prevalence. Fortunately, all models created here were for comparatively rare biota. Qualitative evaluation revealed that the three genera occupied somewhat different parts of the study area. A combined plot of each genus showing only where suitability was greater than MCSS indicated only a small area in the region south of the Lahaina Pinnacles where suitable habitat overlapped for all three genera (black area in Figure 3.15). Outside the area of overlap, *Porites* suitability was dominant 2-3 km off of Lahaina, *Montipora* suitability dominated 3-4 km south of Hekili Point, and *Leptoseris* suitability was dominant along the ridges 6-9 km offshore around Hekili Point. Many areas are evident

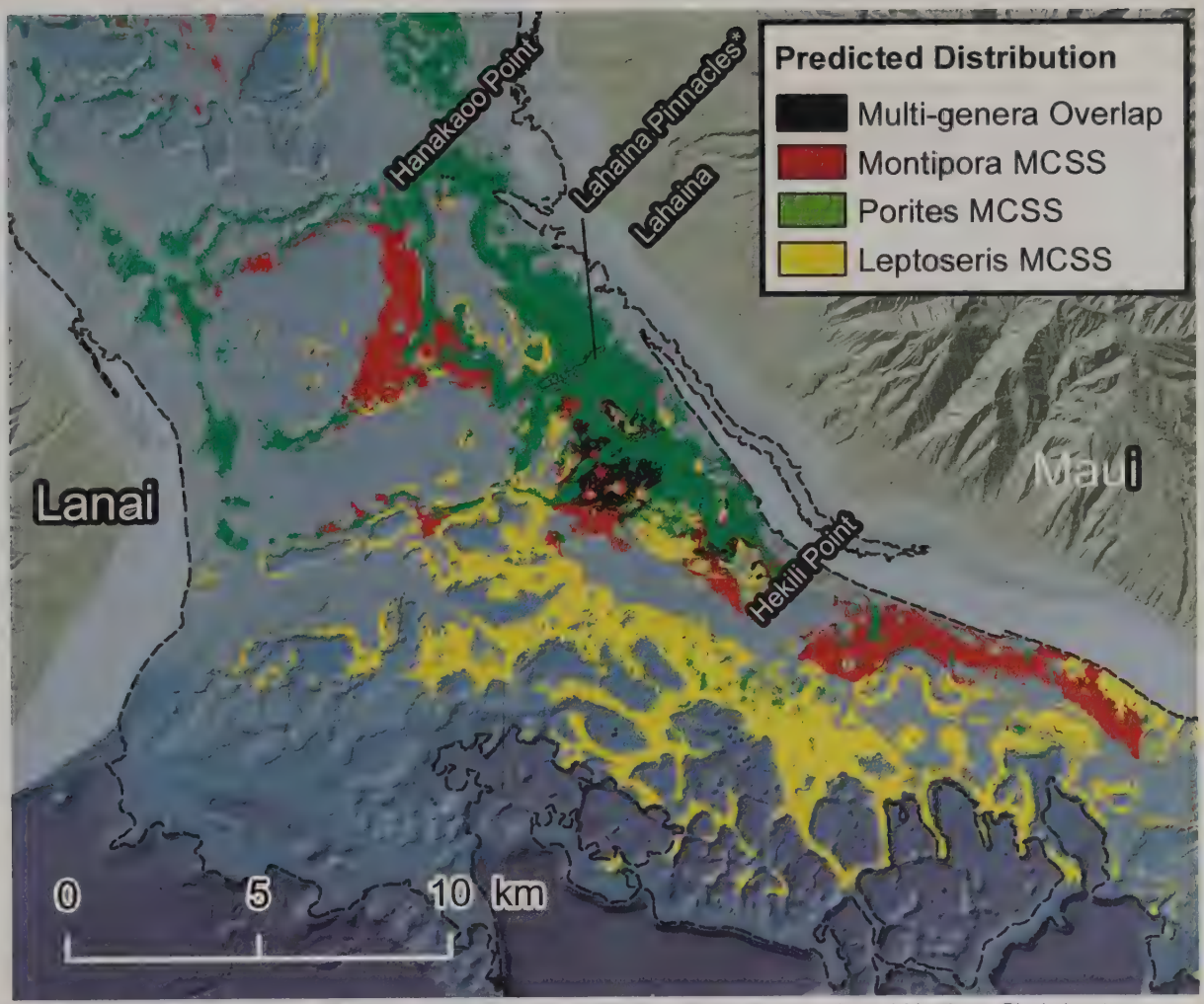

Figure 3.15. Predicted distribution of suitable habitat (based on MCSS) for *Porites*, *Leptoseris*, and *Montipora*. Black denotes co-occurrence of suitable habitat for all three genera. * denotes feature described in Grigg et al. 2002.

where the three genera occupy adjacent but not overlapping bands of suitable habitat. This highlights habitat partitioning among genera along environmental gradients on the ridges and basin walls of the ocean floor in the Au'au Channel.

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CHAPTER 4: DISCUSSION AND CONCLUSION

4.1. DISCUSSION

4.1.1. Modeled Distribution of Mesophotic Corals

MaxEnt produced accurate predictions of habitat suitability for MCEs, as measured by high values of the test AUC statistic and independent accuracy assessment. The four MaxEnt models developed here show that highly suitable locations for mesophotic hard corals are both relatively rare and distributed unevenly in the Au'au Channel Region. No one environmental variable (tested here) fully explained why suitable MCE habitat was clustered in certain locations. However, eight predictors were identified as being important for predicting suitable MCE habitat across three of the four MaxEnt models, and four of these same predictors were important to all of the MaxEnt models. Some of these eight predictors had positive relationships with MCE habitat suitability (within certain thresholds), while others had negative relationships. Habitat suitability for each coral model overlapped across the range of predictor values examined here, although peak suitability occurred at different values of the predictors for different groups. A more detailed discussion about these eight predictors, the differences and similarities in peak suitability among genera, and their influence on habitat predictions by geographic region is located below.

Image 4. Clouds of small reef fish hover over a reef of mixed corals, algae and sponges at a depth of 226 ft. Photo Credit: J. Rooney.

4.1.2. Southeastern Au'au Channel

The majority of suitable habitat for all MCEs and for *Montipora* is predicted to be on the southeastern side of the Au'au Channel between Lahaina Roads Basin and Papawai Point. This southeastern area is characterized by relatively warmer (at the surface), moderately deep and less turbid waters than parts of the north, west and southwest Au'au Channel and the Au'au Channel Region as a whole. Euphotic depth, which is a proxy for both PAR and turbidity, also appears to be less variable in this southeastern location than in most parts of the study area, remaining consistent (> 1% PAR depth within ± 2.3 m) over a six year period from 2004 to 2010. Water temperature measurements taken near this area in 2001 indicate that this layer of warm water (around 26 °C) may be fairly stable down to about 60 m, after which it drops to around 23 °C around 111 m (Figure 4.1; Grigg 2006). The variation in temperature profiles down to 60 m is similar to the temperature variation seen in the SST imagery (i.e., ± 0.9 °C). These numbers and patterns suggest that SST may be a proxy for warmer water down to approximately 60 m in depth, although more measurements are needed to better characterize tidal and seasonal influences on the spatial and temporal heterogeneity of water temperature at

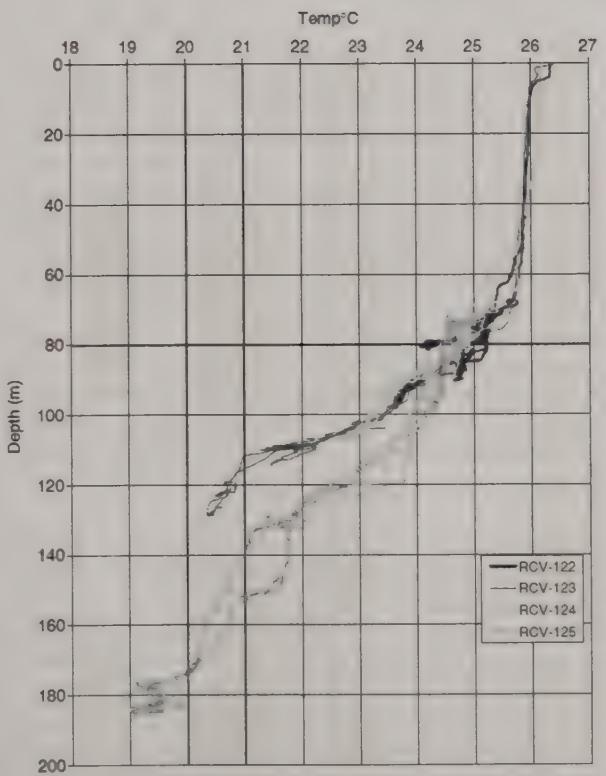

Figure 4.1. Four full-water column temperature measurements taken on November 28, 2001 in the middle of the Au'au Channel between Maui and Lanai. Figure adapted from Grigg 2006.

depth. For MCEs (in general) and *Montipora* (specifically), these environmental trends suggest that on the whole these two groups prefer relatively warmer, moderately deep waters that remain optically clear and stable through time. These habitat preferences are highlighted by the jackknife results, which show the highest habitat suitability values for all mesophotic corals together and *Montipora* specifically occurred at moderate depths (70 and 59 m, respectively) and in warmer (26.22 and 26.13 ° C at the surface), clearer (>1% PAR depth of 103 m) waters (Figure 4.2). It is interesting to note that *Montipora* is considered to be a habitat generalist (Maragos 1977). The fact that *Montipora's* preferences closely mimic those of all mesophotic corals (included in this model) seems to reinforce this concept, and may help explain why it is the only genus whose spatial patterns predominantly follow those of the general mesophotic coral model.

These depth preferences and thresholds are in close agreement with the findings of Rooney et al. 2010, which reported that cover of hard mesophotic corals peaked at approximately 60 m, and that *Montipora* was one of the most common coral genera found in 50 to 80 m of water. However, these thresholds differ from the results reported by Kahng and Kelley 2007, which found *Montipora* to be rare in the 50 to 80 m range. It is interesting to note that the ROV transects in the Au'au Channel analyzed by Kahng and Kelley did not intersect with the spatial distribution of highly suitable *Montipora* habitat predicted by MaxEnt. This geographic mismatch suggests that Kahng and Kelley may have sampled in areas with relatively poor ambient conditions for *Montipora* or a different range of environmental variables than were included in this study. It is very possible that these environmental variables (especially depth, distance to shore and SST) are proxies for other environmental conditions favorable to MCE and *Montipora* recruitment and growth. For example, depth and distance to shore are most likely correlated proxies for light availability, since generally speaking, the seafloor becomes deeper and the water becomes less turbid further from land. Kleypas et al. 1999 found this same positive correlation between PAR and distance from shore when comparing nearly 1,000 reef locations around the world. High SST may be a proxy for calm, low runoff, low turbidity waters. The area of highest SST overlaps with the relatively windless, low rainfall, low wave energy, leeward side of west Maui.

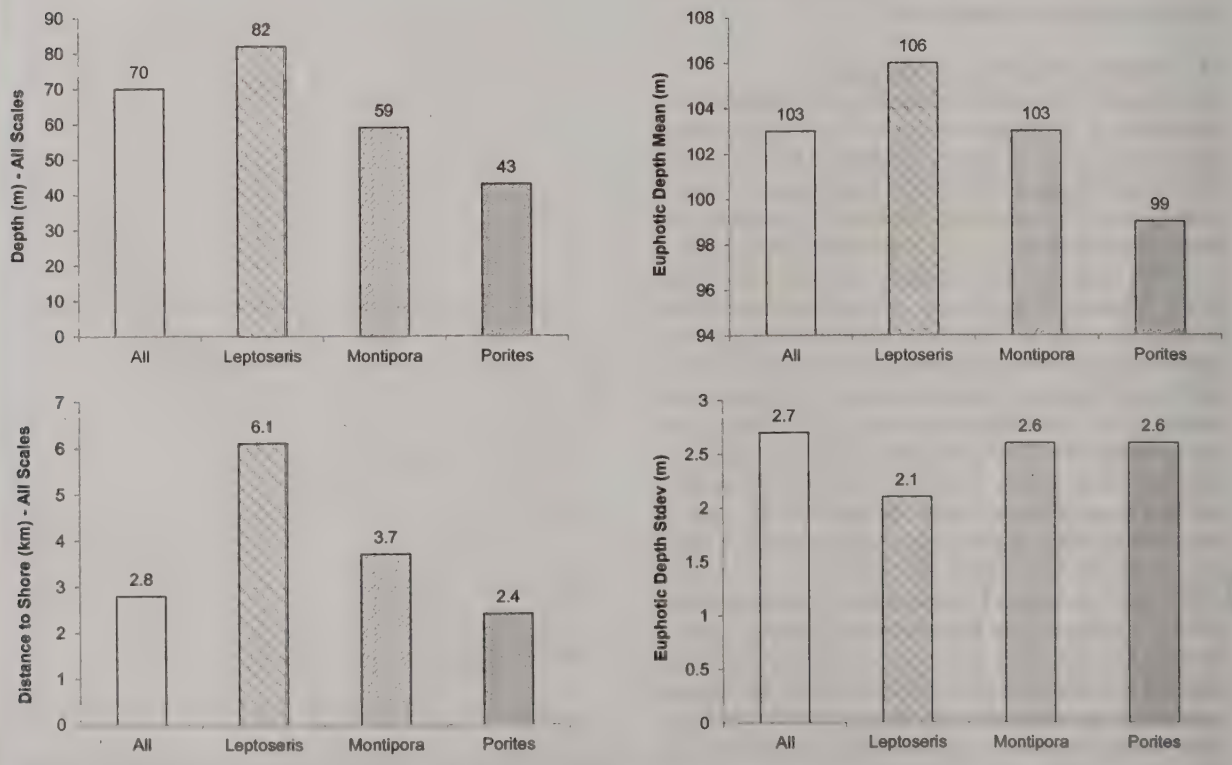

Figure 4.2. The dependence of maximum predicted suitability values on the four most important predictors (i.e., depth, distance to shore, euphotic depth mean and euphotic depth stdev) for all four models. These values are based on the single variable response curves. The predictor value that resulted in the highest habitat suitability score is located on top of each bar for each model.

4.1.3. Eastern Au'au Channel

The majority of suitable habitat for *Porites* is predicted to be on the eastern side of the Au'au Channel between Hanakaoo and Launiupoko Point. Similar to the southeastern area described above, this area is characterized by relatively warmer, slightly shallower and less turbid waters than found in other parts of the study area. Based on the temperature profiles reported above (Grigg 2006), temperature most likely remains within the tolerated range for some species of *Porites* down to over 100 m in this area (Kleypas et al. 1999; Kahng and Kelley 2007). It is also important to note that turbidity levels vary slightly more (> 1% PAR depth within ± 2.7 m) and SST varied slightly less (±0.33°C) in this area than in locations further to the south where the Au'au and Kealaikahiki Channels meet. Collectively, these environmental suitability trends suggest that *Porites* prefers shallower waters than *Montipora* and all mesophotic hard corals combined. These depth preferences agree with the findings of Rooney et al. 2010, which reported that depths from 30 to 50 m were dominated by several shallow water coral species, including *Porites lobata*. They also agree with the results of Grigg 2006, which reported that whereas *P. lobata* can grow at depths up to 100 m, it is more common to find this species at depths shallower than 50 m since reef accretion ceases below this depth threshold.

Image 5. Close up view of a mesophotic reef dominated by branching *Montipora capitata* corals with a few *Leptoseris* corals mixed in, although this depth is shallower than where they are typically encountered. Photo Credit: J. Rooney.

Given these consistent depth preferences, it is likely that *Porites* is limited by the availability of PAR more so than by temperature (Grigg 2006; Kahng et al. 2010) or by any other predictor included in this study. This relationship is not new, as the depth limit of reef building corals has long been associated with decreasing PAR (Wells 1957; Dustan 1975; Kleypas et al. 1999). Even though *Porites* distributions may primarily be limited by light, the MaxEnt output model also suggests that *Porites* can tolerate slightly more turbid (although still exceptionally clear) waters than either *Montipora* or all hard corals combined. This increased resilience agrees with the findings of Piniak 2007, who reported that *Porites lobata* experienced less tissue damage from sedimentation than did *Montipora capitata* because of its more rugose morphology. These habitat preferences are quantified by the jackknife results, which show the highest habitat suitability values for *Porites* occurred at comparatively shallow depths (43 m) and in the most turbid waters (>1% PAR depth at 99 m) out of any of the models. *Porites's* highest habitat suitability values were also located the closest to shore (2.4 km), likely because distances closer to shore are correlated with and a relatively good proxy for decreasing depth, increasing turbidity and increasing variability in PAR. In addition to distance to shore, it is also likely that other predictors, notably depth, are proxies for environmental conditions favorable to *Porites* recruitment and growth that were excluded from this analysis.

4.1.4. Southern Au'au Channel

The majority of suitable habitat for *Leptoseris* is predicted to be in the southern part of the Au'au Channel close to where it meets with the Kealaikahiki Channel. This area has similarly warm water temperatures as in the eastern and southeastern areas discussed above. However unlike these two areas, the southern part of the Au'au Channel had deeper waters on average. It also has the most consistently warm (26.2 °C) and clear waters (> 1% PAR depth within ± 2 m) compared to any other part of the Au'au Channel or study area as a whole. Also, the water temperature at depth most likely remains within the tolerated range for *Leptoseris* (i.e., > 19 °C) down to 120 m in this area (Grigg 2006; Kleypas et al. 1999; Kahng and Kelley 2007). Collectively, these environmental trends suggest that *Leptoseris* prefer slightly deeper, substantially less turbid and less variable waters (in terms of turbidity and, possibly, temperature) than *Montipora*, *Porites* and all hard corals combined. These habitat preferences are quantified by the jackknife results, which show the highest habitat suitability values for *Leptoseris* occurred at the deepest depths (82 m), in the least turbid (>1% PAR depth at 106 m) and least variable waters

(>1% PAR within ± 2.1m and SST ±0.33 °C) compared to any of the other models.

Image 6. Photo from a benthic transect over a reef of *Leptoseris* corals interspersed with *Halimeda* algae at a depth of 250 ft. Photo Credit: J. Rooney.

These depth preferences and thresholds are in close agreement with the findings of Kahng et al. 2010, which reported that *Leptoseris* were commonly found in the deepest parts of the mesophotic zone across the Pacific. They also agree with those of Rooney et al. 2010 and Kahng and Kelley 2007, which documented that the hard substrata between 80 to 90 m was dominated by aggregations of *Leptoseris*. However, *Leptoseris* has been recorded at deeper depths in the MHI, including at 131 m and 153 m near Penguin Banks and Kealakekua Bay, respectively (Kahng and Maragos, 2006; Kahng and Kelley 2007). *Leptoseris's* presence at these exceptionally deep depths suggest that temperature is not a limiting factor for its growth in Hawaii (Kleypas et al. 1999; Kahng and Kelley 2007), even though temperature at the water surface was identified as an important predictor in this modeling process. Therefore, SST (especially standard deviation) is most likely a proxy for another environmental variable describing the stability of the water conditions in the area. The availability and stability of PAR was identified as one of those stable conditions by MaxEnt. *Leptoseris's* preference for less turbid and more optically stable waters also aligns with the findings of Kühlmann 1983, which showed that corals with flat morphologies (like *Leptoseris*) are poorly adapted to resist and more sensitive to sedimentation (Kahng et al. 2010). These flat morphologies are also less effective for passive suspension feeding than the branching structure of many azooxanthellate corals (Kahng et al. 2010). Despite potentially being less effective at heterotrophy and more susceptible to sedimentation, the flat, plate-like morphologies and dark brown pigmentation of *Leptoseris* and other mesophotic corals have advantages, including being specialized for capturing the maximum amount of light (Kahng and Kelley 2007; Kahng et al. 2010).

In addition to being found most commonly at the deepest depths, *Leptoseris's* highest habitat suitability values were also located the furthest from shore (6.1 km), likely because distance to shore is correlated with and a relatively good proxy for increasing depth, decreasing turbidity and reduced variability in PAR (Kleypas et al. 1999). In addition to these four predictors, rugosity and slope of slope (both at 200 m scales) were also important for predicting *Leptoseris* distributions. None of the other MaxEnt models identified seafloor complexity as being important. The *Leptoseris* model's inclusion of these morphometrics suggest that some other variable associated with high complexity, such as available hardbottom, may also play a role in determining the distribution of *Leptoseris*. Competition for space appears to be less of a factor in the mesophotic zone (Avery and Liddell 1997), since macroalgal abundance decreases significantly with increasing depth (Kahng et al. 2010). This may lead to a situation in which the total amount of available hardbottom becomes an important driver of coral distribution. This hypothesis is in keeping with the results of Kahng and Kelley (2007), which suggest that the availability of hardbottom may be a limiting factor for *Leptoseris* to colonize depths below approximately 90 m. It may also explain why *Leptoseris* is not found in the southwestern part of the Au'au Channel, which appears to have similar depth, temperature and turbidity conditions as the southern and southeastern parts of the Channel. Further analysis of the ROV data used for this modeling exercise showed that this southwestern area had less hardbottom on average than the southern part of the Au'au Channel (i.e., 1.3% ±11.0% versus 5.5% ±22.4%, respectively).

4.1.5. The Au'au Channel Region

The Au'au Channel is a unique location among the islands of Maui, Kahoolawe, Lanai and Molokai. It is unique, not only in terms of its geology (Grigg et al. 2002), but also in terms of its physical oceanography and local weather patterns (Fletcher et al. 2008), making it an optimal environment for coral growth (Grigg 1982). There are several physical conditions that help make the Au'au Channel (specifically the southeastern portion) an ideal place for mesophotic hard corals. These conditions include having consistently good water quality and clarity

because it is flushed by tidal currents semi-diurnally; the amount of sediment run-off from the nearby land (i.e., notably between Launiupoko and Papawai Points) is lower than in other parts of Maui (Grigg 2006; Fletcher et al. 2008); and the sediments that do enter the water column are not continually resuspended because this area is largely protected from seasonally strong wind and wave energy. Being protected from this strong wind and wave energy is also important because it creates conditions favorable to faster rates of coral accretion (Dollar 1982; Dollar and Tribble 1993; Grigg 1998), and because it reduces the amount of mixing that occurs in the water column during the summer. This reduction in mixing may allow the water column to warm more uniformly (as seen in the summer water temperature profiles by Grigg 2006), pushing the thermocline (below the one seen at ~5 m) deeper than in other nearby locations. Combined, these oceanographic and weather conditions create patches of comparatively warm, calm, clear waters that remain relatively stable through time.

Although there were some slight differences among the MaxEnt models, these three environmental conditions (i.e., warm, clear and consistent water conditions) were the most important variables for predicting the distribution of mesophotic hard corals. This trend may help explain why the distributions of all hard corals, *Leptoseris*, *Montipora* and *Porites* fell primarily between Hanakaoo and Papawai Points, which appear to have the most stable local weather and water conditions in the Au'au Channel. This environmental stability occurs for a number of reasons, including being wholly sheltered from the damaging North Pacific waves and strong trade winds by the western Maui mountains. Shielding from strong winds and large waves may explain why a consistently warm mass of water sits between these two points almost year round. Water quality conditions appear to be equally stable in this location, and remain consistently clear year-round. Lower amounts of rainfall and lower amounts of urban and agricultural development in the adjacent coastal watersheds may help explain why the area between the Hanakaoo and Papawai Points area is not as turbid as areas to their north and south.

While these regional environmental conditions seem to explain mesophotic coral distributions very well at the scales examined in this study, it is also highly likely that historical events (e.g., the coral harvesting for jewelry) and several other biological and ecological factors, including predation, inter/intra-species competition and recruitment, have and are playing a significant role in shaping distributions, especially at finer spatial scales. However, the influence of these biological and ecological forces on the spatial heterogeneity and species diversity of mesophotic corals is poorly understood, and may change based on species, depth, location and scale. For example, Kahng and Kelley (2007) documented competition for space between *Halimeda* and *Leptoseris* above 80 m, as well as between zooxanthellate and azooxanthellate corals below 90 m in the Au'au Channel. Also, the introduced species, *Carijoa riisei*, has been reported to compete with native black corals in this same location (Kahng and Grigg 2005). These two types of competition would most likely have the greatest impact on *Leptoseris*. More research needs to be conducted examining how these forces shape mesophotic coral community assemblages.

4.2. MANAGEMENT APPLICATIONS

Managers must first understand the spatial distribution of habitats and organisms before they can devise appropriate strategies to manage them. Where are important habitats found? How abundant are species of concern? What threats are located near key resources? How do key resources overlap with each other? Do existing regulations effectively promote resilience of important biota or do management plans need to be updated to reflect a new understanding of present conditions?

This study quantified the rarity and predicted spatial extent of MCEs within an existing MPA. The entire study area is encompassed by one section of the HIHWNMS. The findings contribute to the Sanctuary goal of identifying additional resources and ecosystems of national significance (Oceans Act 1992, NMSP 2002, HIHWNMS and DAR 2007). Knowledge of where MCEs occur within the Sanctuary informs potential modifications to management plans.

Results can be used to identify large areas of high suitability by genus or to target conservation actions in limited but diverse areas where all three genera are predicted to overlap. Results can not only be used to delineate subzones within the sanctuary if special regulations are needed to protect MCEs, but also to target and promote research and educational activities on these important and rare habitats. The georeferenced prediction maps may also be evaluated together with the spatial distribution of other biota (e.g. whales) or human activities to devise ways to minimize conflicts in areas with many overlapping resources and uses. Seafloor planning for any

type of development such as outfall pipe positions, cable routing, mooring/anchoring areas, and other seafloor uses will rely on this type of information to minimize harmful impacts.

Marine spatial planning will become increasingly important for MCEs over the next decade as Hawaii works towards meeting it sustainable energy goals. The application of this type of model may aid many areas outside as well as within the HIHWNMS. Agencies such as the State of Hawaii Departments (including Department of Business, Economic Development and Tourism, Department of Land and Natural Resources and Department of Health), U.S. Department of the Interior's Bureau of Ocean Energy Management, NOAA's Ocean and Coastal Resource Management, and the U.S. Army Corps of Engineers all play a role in supporting, authorizing and/or licensing projects or their components for clean energy development in Hawaiian Waters. Future work could apply this modeling approach to other areas in order to assist with broader marine spatial planning needs.

Important to consider in any application is selecting an appropriate level of habitat suitability. For some management decisions it may be desirable to know only where the most highly suitable MCE habitats are located. For others, it may be beneficial to also consider predicted locations of moderately suitable habitat. MaxEnt offers two ways of adjusting model sensitivity (i.e., the probability of correctly identifying true presence locations) and specificity (i.e., the probability of correctly identifying true absence locations). One way in which model sensitivity and specificity can be adjusted (before model development) is through tuning the regularization parameter. In this study, we have kept the regularization multiplier (beta) fixed at its default value of 1 for simplicity. Larger values of the regularization parameter create simpler, smoother models that are not constrained as tightly to match environmental conditions at observed presence locations. This can be useful when trying to create models that generalize well to new study areas, or when tuning model predictions against independent accuracy assessments, but it is a complex subject and should be used only with care and a thorough understanding of MaxEnt's regularization scheme (Phillips and Dudík, 2008; Warren and Siefert 2011).

A second way in which model sensitivity and specificity can be adjusted (after model development) is through the selection of a particular habitat suitability threshold value (between 0 and 1), above which areas are classified as "suitable." We demonstrate how the choice of this threshold affects errors of omission and commission. Depending on the application, it may be more important to correctly identify locations of coral presence. For example, researchers interested in studying MCEs will want to be able to reliably locate those communities. For other applications, it may be better to accurately know where coral is likely to be absent. For example, companies installing undersea cables will want and need to reliably avoid those communities. A more balanced approach that equates sensitivity and specificity may be most appropriate for other applications not discussed here.

Future efforts should examine how to optimize the habitat suitability thresholds for different applications within the HIHWNMS. One possibility for tailoring the suitability thresholds is to use different combinations of sensitivity and specificity in the MaxEnt ROC curve (Fielding and Bell 1997; Liu et al. 2005). Two threshold methods have been found to perform the best when trying to balance sensitivity and specificity (Liu et al. 2005). The first method is called equal test sensitivity and specificity. This method finds the point on the ROC curve where the difference between the ratio of correct presence records and the ratio of correct absence records is minimized. In this study, we used the second method, called maximum test sensitivity plus specificity or MCSS. This method finds the point on the ROC curve where the sum of the ratio of correct presence records and the ratio of correct absence records is maximized. Both of these threshold selection methods are appropriate if the costs of false positive and false negative predictions are weighted equally. However, it is important to note that these sensitivity/ specificity threshold selection methods are not without biases, and need to be used with caution (Manel et al. 2001). Caution is particularly needed when dealing with rare species because their suitable habitat is almost always over predicted (Manel et al. 2001; Elith and Graham 2009). However, habitat over-prediction can be mitigated by using datasets with unbiased estimates of prevalence or model outputs that describe the probability of occurrence (Polansky et al. 2000; Loiselle et al. 2003). Both of these solutions require samples that are systematically acquired, and not haphazardly acquired (data used in this study were closer to haphazard). Options for future, systematic sample designs are discussed in Section 4.3.1.

4.3. DATA AND INFORMATIONAL GAPS

At mesophotic depths, more than 800 km of seafloor imagery have been collected across the U.S. Pacific Islands Region, documenting the presence of mesophotic reefs in approximately 50 islands, atolls and banks. However, compared to the Caribbean, MCEs in the Pacific still remain relatively unexplored and their distribution largely unknown. While these models help to fill some knowledge gaps about the distribution of MCEs in the Au'au Channel Region, several data and informational gaps still exist and need to be addressed in the future. Data gaps refer to a lack of spatial data that is needed to make informed decisions. Informational gaps are often the result of data gaps, and refer to a lack of understanding of how the different physical and biological components of the system work and fit together. Despite being one of the most well studied regions in the MHI, the Au'au Channel Region still has both data and informational gaps that occur across several different disciplines and at several different spatial scales. These knowledge gaps are not unique to the Au'au Channel, as similar gaps exist across the MHI as a whole. Many of these gaps remain because of the logistical challenges of accessing, measuring and performing experiments at depth (Kahng et al. 2010).

4.3.1. Data Gaps

In terms of data gaps, large, shallow-water areas close to the shorelines of Maui, Kahoolawe and Lanai as well as across the MHI have not yet been mapped at fine (<5 m) spatial resolution. LiDAR collected by the U.S. Army Corps of Engineers in 1999 and 2000 filled in much of these near-shore areas, but several data gaps still exist in key locations. Baseline information, like high resolution bathymetry, is essential for expanding the geographic scope of spatial models (like the one presented here) because it can be used to describe the structure of the seafloor as well as be used as a proxy for other environmental variables including PAR. More importantly, this type of information is the cornerstone of developing informational products to support the process of ecosystem based management. In the future, efforts should continue to integrate new high resolution depth and backscatter surfaces (as SOEST, PIFSC and USGS have been doing), but also to acquire new data to fill in critical near-shore data gaps and further develop our understanding of ecologically important locations.

Image 7. Divers slowly ascending from the bottom wait at their 30 foot decompression stop after collecting data about mesophotic corals. The regulators hanging down provide surface-supplied oxygen from a dive boat above that the dives will breath during their longest decompression stop at a depth of 20 ft. Photo Credit: R. Boland.

In addition to gaps in environmental information, large gaps also exist in our knowledge about the spatial distribution of mesophotic corals in the MHI as a whole. The data used in this project were collected haphazardly. However, future efforts should focus on systematically sampling depths between 30 and 150 m both inside and outside the existing HIHWNMS boundaries around each of the MHI. Systematic sampling (such as equal random stratification) provides several advantages over haphazard approaches (Hirzel and Guisan 2002) and would help improve future habitat suitability modeling efforts. One advantage is that it would allow future MaxEnt predictions to be properly calibrated. Calibration would allow the MaxEnt predictive output values to be converted to probabilities of occurrence (i.e., how likely a species is present), and would standardize them so that different MaxEnt models are directly and quantitatively compared. A second advantage of systematic sampling is that it would allow the Sanctuary to explore using presence-absence modeling techniques in addition to or in lieu of MaxEnt. These techniques would give the Sanctuary the added capability of predicting the abundance of mesophotic corals (in addition to their presence/absence).

4.3.2. Informational Gaps

Relatively little is known about the suite of factors that influence mesophotic community ecology and structure (Kahng et al. 2010). Despite this informational gap, MCEs have long been considered a default refuge for shallow-water coral reef ecosystems because it is assumed that they are more protected from physical disturbance and more isolated from anthropogenic impacts like fishing and land based sources of pollution. Even if they are more protected from disturbance, it is likely that MCEs are inhabited by depth-generalist coral species, which (in the Caribbean) constitute approximately only 25% of the total coral biodiversity (Bongaerts et al. 2010). This gap leaves a large number of shallow-water coral species at risk. It also clearly indicates that many questions remain unanswered about the ecology of MCEs and their level of connectivity with shallow-water reefs. These questions include, but are not limited to:

Image 8. Diver's eye view of a reef of *Leptoseris hawaiiensis* corals at a depth of 275 feet. Despite the low light conditions evident in the photo the coral growth here is luxuriant. Photo Credit: J. Rooney.

1. What environmental conditions influence and/or limit MCE structure and resilience?
2. How do biological and ecological forces, like predation, competition and recruitment, shape mesophotic ecosystems?
3. How are MCEs different from shallow-water coral reef ecosystems?
4. To what extent can or do MCEs serve as refuges for shallow-water species, including both fish and corals?
5. How susceptible are MCEs to anthropogenic impacts, including climate change?
6. What role should MCEs play in planning for resilient reefs in the future?

To begin to answer these questions, additional studies are needed describing the levels of connectivity and the source/sink recruitment dynamics between shallow and deep populations over time. These studies may also concurrently provide insight into the taxonomy, life history, population dynamics and environmental limits of mesophotic corals, which enable them to survive and thrive at extreme depths. Understanding the environmental limits of MCEs will be particularly critical in the future, since these limits will help us predict how coral reef communities will respond to both local environmental and global climate changes.

4.4. CONCLUSION

Although significant research questions and data gaps remain, the MaxEnt predictive models created here are accurate and can be used for a variety of management, scientific, and education applications. These models quantitatively showed that mesophotic coral distributions are concentrated between Hanakaoo and Papawai Points in the Au'au Channel because this area has some of the most stable, local environmental conditions in the study region, hosting warmer, clearer and calmer water conditions almost year round. Although mesophotic corals are also responding to other environmental and ecological cues beyond the ones discussed here, these mathematic and spatial patterns suggest that other areas in the MHI with local environmental conditions similar to those between Hanakaoo and Papawai Points may also host higher concentrations of hard mesophotic corals. Future research efforts should focus on identifying and systematically sampling these areas both inside and outside the Sanctuary boundaries. Understanding the broader geographic distributions of mesophotic corals will help the HIHWNMS to effectively target ecologically important areas for conservation in support of its ecosystem-based management plans and goals.

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